HEADWATER FISHES AND THEIR UPPERMOST HABITATS: A REVIEW AS BACKGROUND FOR STREAM TYPING

Prepared by:

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Executive Summary

This report is intended to provide a complete monograph of published studies and observational reports on headwater fish and the biological and physical nature of the headwater stream reaches in which they live. The focus is on headwater fishes of Washington, but pertinent literature and reports on the subject from around the world are reviewed and incorporated. My objective was to highlight what is known and what remains to be learned about fish and their habitat at the upstream extent of their distribution in Washington streams. Hopefully, this monograph will serve as a one-stop source of background information for all who work in this State to delineate and understand headwater fish reaches. It should also be useful as a springboard for further research to illuminate the unknowns.

Uppermost Fishes, their Life History, Ecology, and Dynamics

Based on stream typers' reports, the uppermost fish in Washington streams is a resident salmonid in well over 80 percent of the observations. Native cutthroat trout comprise the majority of reports, but native rainbow trout and non-native brook trout are also found. Bull trout have not been reported by Washington stream typers, although they do occur elsewhere as the uppermost fish under certain conditions. Even within the anadromous zone, anadromous fishes have been observed only occasionally at the upper extent of fish distribution. Of nongame fishes, sculpins alone have been reported occasionally as the uppermost fish, although they more frequently co-occur with salmonids at uppermost-fish locations. Lampreys and three-spined sticklebacks have been reported one time each at uppermost fish sites.

Stream-dwelling amphibians frequently inhabit streams above the upper extent of fish distribution, and some species may thrive in the absence of fish. On the other hand, predation on small salmonids and the pressure of competition for scarce food resources have been suggested as factors limiting upstream distribution of fish.

Small body size, retention of juvenile body form and skin coloration throughout maturity, early maturation, low fecundity, and short life span relative to their downstream counterparts are characteristics of headwater and above-barrier salmonids. These "juvenilization" traits have been called responses to isolation or insularization and may confer selective advantage on salmonids living in headwater and above-barrier stream environments. Survival and growth of headwater and above-barrier trout appear to be governed by density-independent factors, as opposed to density-dependent factors governing the population dynamics of downstream populations. Owing to "knife-edge selection," genotypes resistant to downstream migration along with genotypes adapted to density-independent factors may dominate in headwater and above-barrier populations.

The Nature of Habitat, and Fish Utilization of Habitat, at the Upper Extent of Distribution

Based on data from 79 field-verified fish-bearing water boundaries, stream channels large enough to carry a mean annual flow of around 1 cfs (0.03 m³/sec) range 0.5 to 3.5 cfs (0.01 to 0.1 m³/sec) have the potential to produce the minimum amount of food needed to sustain a fish. Streams within this range of mean annual flows also can generate sufficient stream power to produce habitat suitable for a headwater salmonid.

Washington stream typers working upstream of the anadromous zone have found upprmost fish in stream segments with gradients ranging from 3 to 35 percent, although only about 10 percent of

these locations are in segments steeper than15 percent. That range of reach gradients could place these reaches in any one of nine Cupp valley segment types, two Rosgen channel segment types, or three Montgomery and Buffington reach types. At the valley segment and channel segment levels of the stream classification hierarchy, upper-fish reaches may occur in upper valley sidewall and headwall tributaries that comprise the actual headwaters of a basin, and in upper reaches of lower valley sidewall tributaries.

Based on field observations, the steepest reaches capable of harboring fish are of the Montgomery and Buffington *Step-pool* reach type. Only this reach type has within it the types of channel units and microhabitat features that a fish could utilize in a steep-gradient reach. At reach gradients lower than 12 to 15 percent, Montgomery and Buffington *Cascade* and *Bedrock* reach types can also have habitat features headwater fish can utilize. The small pools and pockets utilized by fish in reaches with overall steep gradients themselves have water-surface gradients of less than 4 percent. The typically small adult trout inhabiting these sites probably do not move to downstream locations and habitats as winter approaches, but rather, take advantage of widely available interstitial spaces beneath rubble and boulders at or near their summer locations.

During stream-typing of 306 streams in western Washington, 80 percent of which were in reach gradients of 12 percent or less, three distinct types of of fish-bearing water boundaries were recorded. *At Confluence* boundaries (where a smaller, fishless tributary entered the fish-bearing stream, but fish distribution continued in the main stream beyond the confluence) accounted for about two-thirds of the fish-bearing water boundaries. *Along Channel* boundaries (where stream size and water flows diminished in an upstream direction to a point where fish use ceased) were the next most abundant type. *Tributary Junction* boundaries (where two forks joined to produce the channel being surveyed but neither of the two upstream forks contained fish) was the third type. Regarding

At Confluence boundaries, most of the time some abrupt change in a habitat feature was present to account for cessation of fish use; however, at about 10 percent of these sites no obvious physical cause could be determined. Fish use simply stopped, even though habitat that the stream typers judged to be suitable appeared to be both available and accessible upstream.

The absence of water in stream channels often belies their importance to fish. Fish that utilize intermittent streams move in to spawn when water is present, but are mobile enough so that reconditioned adults and juveniles can move out as the water recedes. Where fish have adapted to intermittent water conditions, stranding may be only minimal.

Delineating the Upper Extent of Fish Distribution

Stream flow, basin area, reach morphology, reach gradient, and microhabitat type appear to be the principal factors affecting the upstream distribution of fish. Additional factors that may also come into play are (1) the often-times four-to six-fold natural fluctuations in fish abundance that may occur from one year to the next in a stream, (2) the natural cycle of disturbance of upstream reaches by catastrophic debris flows which operates on a scale of one to four centuries in Washington drainage basins, and (3) the cycle of drought years in the basin. There is some uncertainty about whether either mechanism (1) or (2) really applies to uppermost fishes because both seem to require a density-dependent response on the part of the fish, whereas available evidence indicates that uppermost fish are governed by density-independent factors. More research is needed to understand these factors better. Mechanism (3) is entirely untested and needs field work to verify.

Aside from the State of Oregon, which relies on the basin area–probability of fish presence methodology, virtually all other approaches to delineating upper extent of fish distribution involve regression modeling to predict fish standing crop. Models incorporating as few as one to as many as

21 input variables have been developed, but common to most are variables that incorporate stream size, gradient, some measure of climate, and some measure of *likely availability of nutrients and* energy. Although coefficients of determination for some of these models are better than 75 percent, the best models appear limited to just the specific areas for which they were developed.

Washington is developing a model using input variables of basin area, reach gradient, elevation, and basin-average precipitation. Coefficient of determination for the current model, which is still being tested, is about 95 percent, i.e., the model makes the correct call in about 95 percent of the cases, and errors are about evenly distributed both pro and con, i.e., the model signals a fishbearing water boundary that is not subsequently found about as often as it fails to call a true boundary that is later found.

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Chapter One — Introduction

"Effective maintenance and recovery of fish habitats and populations requires specific geographic knowledge of existing and potential fish habitats as well as the higher elevation, non-fishbearing stream systems that create and influence them." **(Language in NMFS proposed rule governing "take" of threatened steelhead, Federal Register 64, no. 250: 73479-73506, Dec. 30, 1999)**

Importance of the Uppermost Fish

Much attention has been focused recently at both the state and federal levels on headwater streams and their uppermost fishes. Federal interest is high because, increasingly, headwater tributaries may serve as refugia for rare, threatened, or endangered native fishes (**Gresswell 1988; Young 1995; Duff 1996; Dunham et al. 1999**). Also, as indicated by the language in the chapter header, federal agencies are recognizing that headwater streams, whether fishbearing or not, influence and contribute to the well-being of downstream habitats and populations (**Dalton 1999**).

At the state level, in both Washington and Oregon, one vital issue is how much protection should be given to headwater stream reaches under forest practices rules. Because fishbearing waters generally receive more stringent protection under these rules, the upper extent of fish distribution in a stream — as well as how that point should be identified — is of considerable economic importance.

In the past, headwater reaches were largely ignored in stream typing efforts. Fish use was often presumed to stop at a falls or a steep section of channel, or at a point where channel dimensions fell below some arbitrary minimum size. Reaches upstream of these points were designated non-fishbearing almost by default. That began to change in the early 1990s when biologists with the treaty Indian tribes and certain fish conservation groups reported finding fish much further upstream than the official stream typing maps recognized (**Baxter and Mobbs 1992; Baxter 1993; Bahls and Ereth 1994; S. Conroy, Washington Trout, personal communication 1996**). Fish were being found in small stream reaches with gradients as steep as 31 and 35 percent (**S. Conroy, Washington Trout,**

personal communication 1996; J. Silver, Hoh Indian Tribe, personal communication 1996)—in other words, in places where the conventional wisdom of the time about fish/habitat relationships would have deemed not possible.

One problem with that old conventional wisdom is that most of what we know about fish/habitat relationships is based upon research conducted in downstream reaches—in rivers and streams of low to moderate gradient (generally less than 3 percent) with well-developed pool-riffle morphology (**Kondolf et al. 1991**). One reason for this is that this is where conditions are most favorable and fish population densities are highest and easiest to study. Many assumptions regarding small headwater channels have, therefore, been driven by extrapolation of research done on larger channels (**Liquori 2000**). There is increasing evidence that these extrapolations may not apply to headwater channels or to fish at or near the upper extent of their distribution in streams. Although literature exists, it is widely scattered. There has been no comparable compilation and synthesis of fish/habitat relationships for headwater systems.

Goals and Objectives of this Report

The goal of this report is to provide that missing compilation and synthesis. My objective was to produce a complete monograph of published studies and observational reports on headwater fish and the biological and physical nature of the headwater stream reaches in which they live, in order to highlight what is known and what remains to be learned about these systems. The focus is on headwater fishes of Washington, but pertinent literature and reports on the subject from around the world are reviewed and incorporated. Hopefully, this monograph will serve as a one-stop source of background information for all who work in this State to delineate and understand headwater fish reaches. It should also be useful as a springboard for further research to illuminate the unknowns.

The report is presented in three parts:

- <u>Chapter Two</u> compiles the literature on the biology of uppermost fishes: their life history and ecology, their energetics and population dynamics, and their adaptive genetic uniqueness. Fishes present at the uppermost extent of fish distribution in Washington are listed, as well as other aquatic vertebrates associated with uppermost fish. Also covered is what is known about the headwater occurrence of bull trout.

- <u>Chapter Three</u> covers the literature on the physical nature of habitat and how fish deploy in and use this habitat at the upper extent of fish distribution.

- Chapter Four draws on material from chapters two and three plus material from other disciplines to focus on factors that define the upper extent of fish use. Also discussed here are methods employed and contemplated for delineating the upper extent of fish distribution.

Chapter Two—Uppermost Fishes,
their Life History, Ecology, and Dynamics

Fishes Occurring at the Uppermost Extent of Distribution

Where Washington stream typers have actually brought fish to hand for identification, the uppermost fish in the stream has been some form of resident trout in well over 80 percent of the cases (**Fransen et al. 1998; Simpson Timber Company 1999; M. Liquori, unpublished data 2000**)[1]. West of the Cascade crest, native coastal cutthroat trout *Oncorhynchus clarki clarki* comprise the majority of occurrences, with the balance being coastal rainbow trout *O. mykiss irideus*.[2] On the east side of the Cascade crest, the uppermost native fish may be westslope cutthroat trout *O. c. lewisi* or redband rainbow trout *O. m. gairdneri* [3]. Where found, bull trout *Salvelinus confluentus* too can occur as the uppermost fish in the drainage (**Platts 1979; Ziller 1992; C. Kraemer, Washington Department of Fish and Wildlife, personal communication 2000**) although they have evidently not as yet been encountered by Washington stream typers.

It is quite often the case in the Pacific northwest that rainbow trout (or in the anadromous zone, steelhead) and cutthroat trout both occur in a stream. In such situations, they generally partition the stream with rainbow trout dominating in the lower elevation lower-gradient reaches and cutthroat trout dominating in the higher-gradient reaches near the headwaters (**Hartman and Gill 1968**). For example, in the South Fork Hoh basin, **Sedell et al. (1982)** found that the fish most likely to be found in the upper valley headwall and sidewall tributaries, which they described as mostly step-pool habitat units (see Chapter Three), were resident coastal cutthroat trout. Juvenile steelhead/rainbow trout were found mainly in the main channel of the river, in the terrace tributaries, and in the lower reaches of the lower valley sidewall tributaries. Because of this partitioning, one would not expect to find cutthroat and rainbow trout occurring together as the uppermost fish. Even so, this combination has been reported in at least two instances by Washington stream typers (**M. Liquori, unpublished data 2000**).

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[1] This is not a complete enumeration of last-fish identifications. Under a separate CMER grant, Washington Trout, a coldwater fish conservation organization which has also participated in stream typing, is compiling complete data on its observations. These should be available later in 2000.

[2] I follow Behnke (1992) for classification of rainbow trout, where the coastal form native to drainages west of the Cascade crest is recognized as a distinct subspecies from all forms native to interior drainages.

[3] The interior subspecies recognized by Behnke (1992) as the form native to the mid- and upper-Columbia and upper Fraser River basins.

Although the majority of uppermost fish sites are located high in the headwaters of catchments, well upstream of anadromous barriers, some small streams do head up in low to moderate gradient settings within the anadromous zone and present no physical barriers to anadromous access. In these instances, coho salmon *Oncorhynchus kisutch* and/or sea-run cutthroat trout can extend to the upper end of fish distribution. In their stream typing work involving 306 streams, **Fransen et al. (1998)** reported finding coho alone as the uppermost fish at 2 percent of their sites, and coho occurring together with cutthroat trout at 4 percent of their sites. Adult chum salmon and sea-run cutthroat trout have also been observed spawning at the initiation points of two low gradient, spring-fed tributaries in south Puget Sound (**M. Ereth, Skokomish Tribe Department of Natural Resources, personal communication 2000**).

Brook trout *Salvelinus fontinalis* have been reported as the uppermost fish in a few instances, which brings up the question of introduced species. The brook trout is not a native species here, but has been widely stocked. Brook trout are known to displace native gamefish, and can occupy a stream system by colonizing in an upstream direction provided they do not encounter barriers. Observers in the Rocky Mountain west have reported that brook trout appear to be blocked from ascending reaches of 12 to 15 percent gradient (**Fausch 1989; Bozek and Hubert 1992**), but in work just published **Adams et al. (2000)** found that brook trout can indeed ascend such reaches. They can, of course, also colonize downstream from stocked lakes or ponds above barriers. But the occurrence of brook trout as the uppermost fish in stream reaches inaccessable from below and without headwater lakes or ponds is a sure indicator that stocking of the site has occurred, not colonization. This is not to say that the presence of brook trout should be discounted. They do serve as an indicator of habitat that could be used just as well by native gamefish.

Occasionally, sculpins (*Cottus* spp.) are reported together with trout as a two-fish biome at the upper end of fish distribution in a stream (**Connolly 1996; Fransen et al. 1998; M. Liquori, unpublished data**), and in one instance each, sculpin and coho were reported together (**M. Liquori, unpublished data 2000**) and sculpin and lamprey were reported together (**M. Hunter, Washington Department of Fish and Wildlife, personal communication 2000**) at the upper extent of fish distribution. Sculpins alone have also been found from time to time as the uppermost fish in a stream. In stream typers' data made available for this report, sculpins alone account for about 3 percent of the cases reported (**Fransen et al. 1998; M. Liquori, unpublished data 2000**). In other reports, sculpins alone have been found in headwater tributaries of the Deschutes River (**Bisson 1977**) and in hanging tributaries of the West Fork Satsop River (**M. Ereth, Skokomish Tribe, personal communication 2000**). Most of the sculpins occurring in headwater streams are probably shorthead (*C. confusus*) (**Bisson 1977**) or reticulate sculpins *C. perplexus* (**Krohn 1968; Connolly 1996**), but

riffle sculpins *C. gulosus* too are known to be habitues of the swift currents and conditions typical of headwater stream reaches (**Widoski and Whitney 1979; Mongillo and Hallock 1997**).

Further on the headwater distribution of sculpins, **Connolly (1996)** noted that in the central Oregon Coast Range, streams in sandstone lithology appeared to have a gradient limit to the upstream distribution of reticulate sculpins of about 4 percent, whereas distribution of sculpins was not affected by gradient in basalt streams. Based on his personal observations in the headwaters of southwest Washington streams where both cutthroat trout and shorthead sculpins were widespread, **Bisson (personal communication 2000)** thought it most likely that the absence of one or both forms from certain tributaries was due either to barriers to upstream movement—in one tributary, upstream sculpin distribution stopped at a falls only 0.5 m high but cutthroat trout were present above it, suggesting that even low barriers can be impediments to shorthead sculpins—or to localized catastrophes such as debris avalanches that exterminated entire populations that were later differentially replaced.

The Washington Forest Practices Emergency Rules and Board Manual contains language regarding protection for lampreys. Lampreys have been observed together with sculpins well above the location of the last salmonid in the headwaters of Mill Creek, Wakiakum County, Washington (**M. Hunter, Washington Department of Fish and Wildlife, personal communication 2000**), but to date this is the only verified observation. Other information suggesting that lampreys can occur above the distribution of salmonids is equivocal, as discussed below.

Three species of lamprey occur in Pacific northwest streams: Pacific lamprey *Lampetra tridentata*, river lamprey *L. ayresi* and western brook lamprey *L. richardsoni*. The Pacific and river lampreys are anadromous whereas the western brook lamprey completes its entire life cycle in fresh water (**Wydoski and Whitney 1979**). The Pacific lamprey is the only one found in eastern Washington streams. Although a freshwater resident and habitue of small streams, a curiosity about the distribution of the western brook lamprey is that it apparently does not occur upstream of the limit of anadromous salmonid influence (**R. Bilby, National Marine Fisheries Service, personal communication 1999; B. Fransen, Weyerhaeuser Company, personal communication 2000**), although these observations need to be verified by field work. Conversely, the anadromous forms, the Pacific lamprey in particular, may ascend to headwater areas beyond the upper extent of anadromous salmonids (**Beamish 1980; Farlinger and Beamish 1984; Beamish and Levings 1991**).

In Canada, Pacific lamprey adults have been observed to migrate through rapids and over waterfalls to reach headwater spawning areas (**Beamish 1980**), and ammocoetes (juveniles) of this species were found in extreme headwater creeks of the Bulkley and Kispiox river systems (**Farlinger and**

Beamish 1984). On the other hand, observed spawning sites of Pacific lamprey are invariably described as being in low gradient gravel-bed stream sections, e.g., in tailouts of pools, and nests are generally in water 0.3 m to over 1 m in depth **(Farlinger and Beamish 1984).** As will become clear in Chapter Three, these descriptions are not typical of uppermost-fish locations. Thus, the Canadian references to migrating to extreme headwater creeks and ascending waterfalls may signify more the distance of migration to reach spawning sites and the obstacles overcome along the way, rather than implying that lampreys can occur as the uppermost fish. More field work would help to sort this out.

The only other non-game fish actually recorded by Washington stream typers as the uppermost fish is the three-spine stickleback *Gasterosteus aculeatus*, and this species too has been reported only once. In that case, the sticklebacks occupied wetland habitat above the identified location of the uppermost gamefish **(Fransen et al. 1998).**

The Headwater Occurrence of Bull Trout

Bull trout have been listed as threatened in the coterminous United States **(Barry 1999),** which has triggered a great deal of interest in knowing where and under what circumstances bull trout occur in Washington headwater streams. As noted above, it is known that where found, bull trout may occur as the uppermost fish in a drainage **(Platts 1979; Ziller 1992; C. Kraemer Washington Department of Fish and Wildlife, personal communication 2000).** Based on a search of historical and contemporary records, **Goetz (1994, 1997)** published the map shown in **Figure 1** for bull trout spawning and rearing distribution in Washington and Oregon. He pointed out that when analyzed by geomorphic province,[4] the distribution of bull trout spawning and rearing habitat follows a clear trend, being restricted to the highest relief areas in each state.

But not all high relief areas support (or supported) bull trout spawning and rearing, and even in areas that do (or did), actual distribution could be disjunct or restricted to just certain portions **(Goetz 1994, 1997).** For example:

- Bull trout spawning and rearing has never been recorded from streams in the Klamath Mountain or Coast Range provinces or in the Puget Trough, but spawning and rearing does occur in most river

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[4] Goetz used the **Franklin and Dyrness (1973)[1988]** province delineations but the ecoregion definitions of **Omernik and Gallant (1986)** could be used just as well.
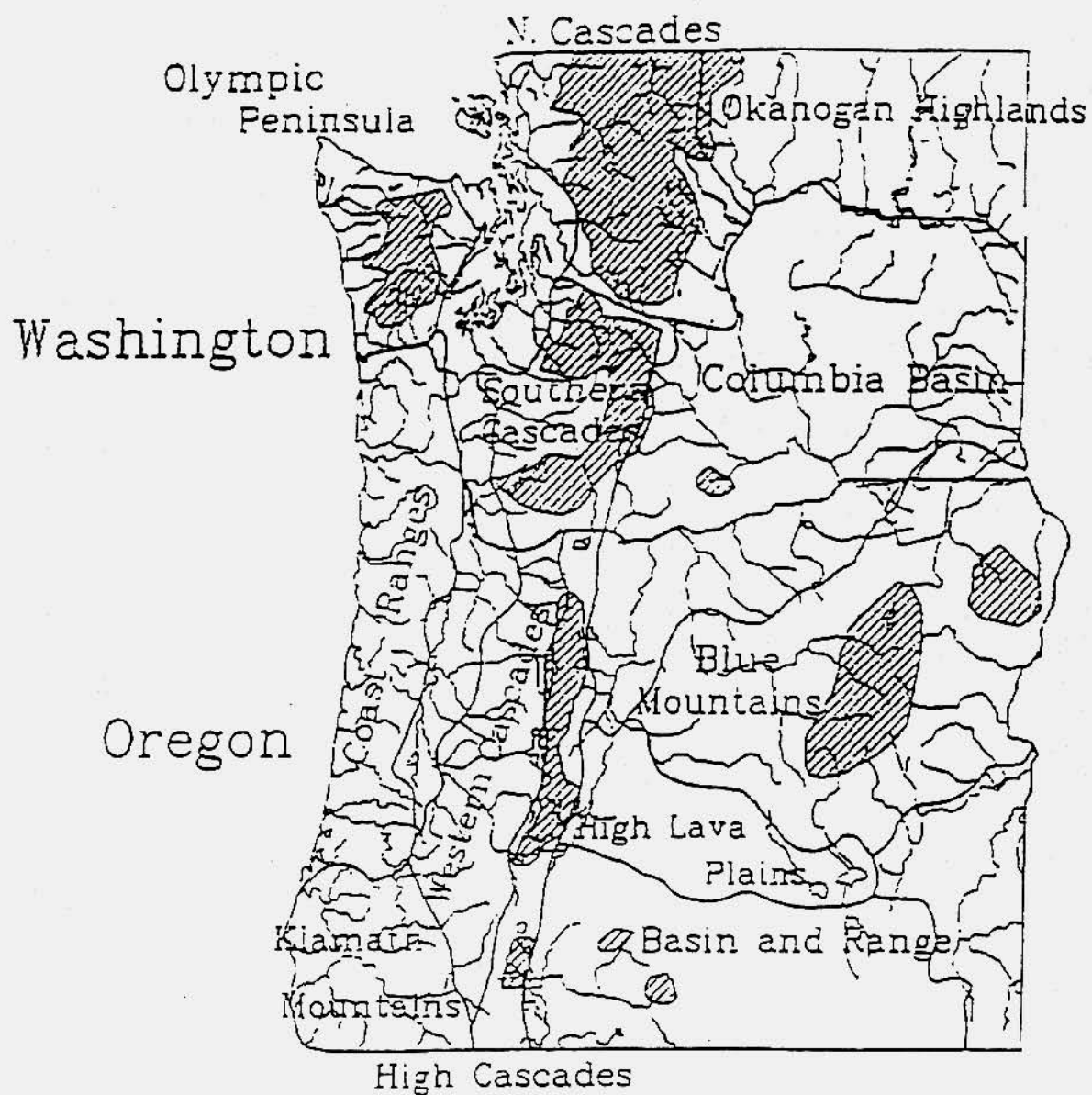
Figure 1. Distribution of bull trout spawning and rearing habitat (hatched area) by geomorphic province in Washington and Oregon. See Goetz (1994) for records on which this map is based.

basins originating in the Olympic Mountains of the Olympic Peninsula province, as well as in the North Cascades province of Washington.

- In the High Cascades province of Oregon, spawning and rearing populations have been recorded in most major drainages from upper Klamath Lake to Hood River, but not in the Rogue or Umpqua River basins.

- In the Southern Washington Cascades province, bull trout spawning and rearing occurs in some (but not all) streams east of the Cascade crest and in the uppermost reaches of most rivers draining Mt. Rainier, but not in the upper Cowlitz (although there is an anthropologist's report from the late 1920s that refers to "Dolly Varden[5]" at the confluence of the Clear Fork of the Cowlitz—see **Costima 1934**). In streams draining west from Mt. Adams, bull trout spawning and rearing occurs only in certain tributaries of the Lewis River in the vicinity of Mt. St. Helens.

- In the Basin and Range province of southeastern Oregon, only two high-elevation "islands" of bull trout spawning and rearing occur, and in these, the bull trout are found only in the uppermost stream reaches. Likewise, in the Blue Mountain province, headwater streams of the Strawberry, Wallowa, and Blue Mountain ranges support disjunct "island" populations. Bull trout have not been recorded from drainages in the High Lava Plains and Owyhee Uplands provinces of Oregon.

In reviewing the information on bull trout spawning and rearing distribution summarized above, **Goetz (1994, 1997)** pointed out that historic and current spawning and rearing habitat areas are in, or closely associated with, cold spring-fed streams. In Washington and Oregon, as well as elsewhere, these are very often located in areas with highly permeable volcanic rock. Cold water temperatures appear to be requisite for bull trout spawning and early life-history stages (**Scott and Crossman 1973; McPhail and Murray 1979; Wydoski and Whitney 1979; Fraley and Shepard 1989; Williams and Mullan 1992**). **Goetz (1997)** suggested that the distributional boundaries for bull trout in Washington and Oregon may be defined by the location of cold, volcanic spring-fed streams. The presence or absence of such springs may explain much of why bull trout occur only in selected 1st and 2nd order tributaries, even within watersheds or provinces normally thought of as within bull trout range.

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[5] Up until 1978, both bull trout and Dolly Varden charr *Salvelinus malma* were classified as one species, *S. malma*. The name Dolly Varden was commonly used for both, although interior fish were often called bull trout. **Cavender (1978)** published results on taxonomy and distribution of bull trout that finally convinced the scientific community of the reality of two distinct species. The "Dolly Varden" referred to in this old ethnographer's report may have actually been bull trout.

Most of the recent work to understand the ecology and habitat needs of bull trout has focused on migratory life-history forms; i.e., fluvial, lake-dwelling, and anadromous populations (**Macay et al. 1997**). Even **Goetz's (1994, 1997)** work, from which Figure 1 was obtained, was primarily concerned with migratory bull trout. Only a few studies to date have addressed stream-resident populations, the life-history form most likely to be encountered in the uppermost reaches of fish distribution. And I could find only one, a study by **Ziller (1992)**, that provided any sort of physical description of the last-fish reaches where bull trout were found.[6]

Ziller (1992) observed bull trout as the uppermost fish in four headwater tributaries of the Sprague River, Klamath Basin, Oregon. Most of the bull trout he encountered were less than 190 mm in fork length (FL); the smallest fish was only 40 mm FL. Bull trout were the only fishes occupying reaches at the upper extent of fish distribution in each stream, giving way to rainbow trout and/or introduced brown trout *Salmo trutta* in lower-gradient, lower elevation downstream reaches. Elevations at the upper limits of bull trout distribution in the four streams ranged from 1,844 m to 2,048 m, and reach gradients were steep—Ziller published graphs of elevation vs. longitudinal distance from the source for each stream, from which I obtained reach gradient values of 7.5, 10, 20, and 22.5 percent for the four last-fish reaches. Substrate and cover were similar in all four bull trout-only reaches, and consisted of rubble/cobble substrate with turbulence and LWD as the dominant cover elements. The bull trout-only reaches were quite cold, with minimum daily water temperatures (measured from mid- or late August through the first week of September) ranging from 3.5° C to 6.1° C, and maximum daily water temperatures (measured over the same periods) ranging from 10° C to 14° C.

Other Aquatic Vertebrates Associated with Headwater Stream Reaches

In many headwaters and small, high gradient streams of the Pacific northwest, amphibians are the predominant vertebrate present (**Murphy and Hall 1981; Nussbaum et al. 1983; Bury 1988; Corn and Bury 1989**). Amphibians have been reported to comprise more than 90 percent of the total predator biomass in some of these systems (**Murphy and Hall 1981**). In surveys of a number of 1st- and 2nd-order streams in unmanaged, naturally regenerated young, mature, and old-growth forests in Oregon and Washington, **Bury et al. (1991)** found aquatic amphibians to be ten times more abundant with four times the biomass than what has been reported for salmonids in similar streams (Bury et al.

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[6] Under another grant from CMER, Washington Trout will send field crews into the headwaters of two basins known to be inhabited by bull trout. These are the upper Elwha River basin on the Olympic Peninsula and the Suiattle River basin in the North Cascades. The objective of this work is to locate and describe uppermost-fish reaches in settings unaffected by man-caused disturbances.

did not measure salmonid densities and biomasses themselves, but used values compiled by **Platts and McHenry (1988)** for their comparison).

Three types of salamanders plus the tailed frog *Ascaphus truei* are associated with small headwater stream reaches (**Bury and Corn 1991; Bury et al. 1991; Leonard et al. 1993; Blaustein et al. 1995; Richardson and Neill 1998**):

- Pacific giant salamander *Dicamptodon tenebrosus* and/or Cope's giant salamander *D. copei* (formerly these were considered a single species, *Dicamptodon ensatus*). Giant salamanders, whose larvae are aquatic, are generally the most likely amphibians to be found co-habiting with fish in headwater reaches, but the most abundant populations of these species occur in small streams lacking fish (**Richardson and Neill 1998; M. Liquori, Champion Pacific, Inc., personal communication 2000**). **Fransen et al. (1998)** observed *Dicamptodon* young-of-the-year (YOY) in much greater numbers immediately above fish-bearing water boundaries than elsewhere in streams containing these salamanders.

- Tailed frog. Tailed frogs are generally the second most likely amphibians to be found in headwater reaches with fish but, like the giant salamanders, the most abundant populations occur in small streams lacking fish (**Richardson and Neill 1998**).

- Torrent salamanders *Rhyacotriton* spp. This group was formerly considered a single species, but has now been split into four, each found in a different locale: (1) Olympic torrent salamander *R. olympicus* (Olympic Peninsula); (2) Columbia torrent salamander *R. kezeri* (Willapa Hills and northern Oregon Coast Range); (3) Cascade torrent salamander *R. cascadae* (southern Washington and northern Oregon Cascades); and (4) southern torrent salamander *R. variegatus* (extends up from the south through the central Oregon Coast Range, but not into Washington). Torrent salamanders appear to be specialized for a life in cold water and are often found in seeps and around waterfalls and splash zones in streams.

- Several salamanders of the genus *Plethodon* also occur in association with small streams, usually in wet rock rubble along stream edges. However, these salamanders lack the aquatic larval stage and develop into adults directly from eggs. Whether they interact with fish in the stream is a question. Those most likely to be found near the upper extent of fish distribution include: (1) western red-backed salamander *P. vehiculum* (a species widespread in the Pacific northwest): (2) Van Dyke's salamamder *P. vandykei* (found only in Washington, but in three distinct regions: the South Cascades, Willapa Hills, and Olympic Peninsula); and (3) Dunn's salamander *P. dunni*

(occurs in Oregon Cascades and Oregon Coast Range provinces and to some extent in the Willapa Hills of Washington).

Larvae of the Pacific giant salamander and/or Cope's giant salamander co-occur with early life-stages of anadromous salmonids in some streams, and with all life-stages of resident salmonids in the upstream reaches of concern to us here. The opinion has been expressed that competition or predation pressure from salamander larvae may come into play in limiting the upstream distribution of fish (**M. Liquori, Champion Pacific, Inc. personal communication 2000**). On the flip side, fish predation on salamander larvae and tailed frog tadpoles is often mentioned to explain why densities of these amphibians are often so much higher in streams just above the last fish (**Fransen et al. (1998; M. Liquori, Champion Pacific, Inc., personal communication 2000**).

Larval salamanders, like salmonids, are gape-limited predators that include larger prey items in their diet as they grow (**Antonelli et al. 1972; Parker 1993, 1994**). The threshold size for a larval *Dicamptodon* to be able to capture and ingest a juvenile salmonid is about 88 mm total length (TL), which they attain by the end of their first year (**Parker 1993**). This is also about the size at which they outgrow the ability of resident trout to capture and ingest them. Thus, while YOY *Dicamptodon* may be preyed upon by larger salmonids, by the end of their first year they are likely to have outgrown that predation risk and can prey on juvenile salmonids in return. **Parker (1993)** was able to observe three actual captures of YOY salmonids by Pacific giant salamander larvae in the wild. A common feature of each capture was that the fish were ambushed by larger salamander larvae that were initially under cover. He suggested that a key factor likely to influence the interaction between larval salamanders and juvenile salmonids is the overlap in their use of microhabitats, particularly their use of similar cover objects. He noted that crevices among large stones and under large organic debris are used as cover by both. A question he asked (but did not answer) was, can juvenile fish detect the presence of large salamanders under specific cover objects and avoid those objects as a means of reducing predation risk?

Parker (1993, 1994) did learn that larval *Dicamptodon* feed predominantly on benthic macroinvertebrates and terrestrial invertebrates that fall into the stream, corroborating earlier studies by **Metter (1963)** and **Antonelli et al. (1972)**. Individual larger prey, such as juvenile salmonids, were uncommon in larval salamander stomach contents. Those that were found averaged 32 mm in standard length (SL) and ranged from 21 mm to 46 mm SL, and the majority were found in samples collected in spring and early summer, suggesting that the importance of salamander predation on salmonids may be restricted seasonally (**Parker 1993, 1994**).

Antonelli et al. (1972) focused on the competition aspect between fish and larval salamanders. While larval *Dicamptodon* and juvenile salmonids are both opportunistic feeders, **Antonelli et al. (1972)** found that larval *Dicamptodon* feed almost entirely on benthos while juvenile salmonids feed on organisms throughout the water column. They concluded that competition for food resources could occur, but is relaxed somewhat by this diversity of feeding habits.

Life-History, Energetics, and Dynamics of Headwater Salmonids

Because the large majority of uppermost fishes are resident salmonids, the remainder of this chapter will focus on them.

Resident salmonids found at or near the upstream end of their distribution in streams seldom grow very large (**Blackett 1973; Nicholas 1978; Jonsson and Sandlund 1979; Tsao 1979; Northcote and Hartman 1988; Ziller 1992; House 1995; Sabo 1995**). Maximum length rarely exceeds 200 mm, and is very often substantially less than that. One reason offered for this is that these fish occur at or very near the limit of available stream resources. In order for a fish to persist at a given location in a stream, it needs two essential resources: physical habitat and food. If *either* is lacking, the fish cannot persist there, let alone grow to a large size.

In addition to small overall size of individuals, average salmonid densities and biomasses are much lower—often 5 to 100 times lower—in above-barrier and headwater reaches than in reaches with anadromous access (**Northcote and Hartmann 1988**). The biomass data shown in **Figure 2** are typical of upper stream reaches in the Pacific northwest—and of course, these values decline to zero at the upper extent of fish distribution. Low densities and biomasses too may be associated at least in part with low food availability.

Many studies have demonstrated strong food limitations in Pacific northwest streams (**Warren et al. 1964; Mason 1976; Bisson and Bilby 1998**). Headwater sections of Pacific northwest streams are often characterized by closed forest canopies with their primary energy source coming from allochthonous inputs of coarse particulate organic matter (CPOM). The macroinvertebrate populations that comprise the food base for salmonids in such stream sections consist predominantly of shredder organisms that feed on CPOM (**Vannote et al. 1980; Hawkins and Sedell 1981; Triska et al. 1982**). But total invertebrate production in these higher stream reaches is substantially lower than in downstream reaches with anadromous access (**Northcote and Hartmann 1988**).
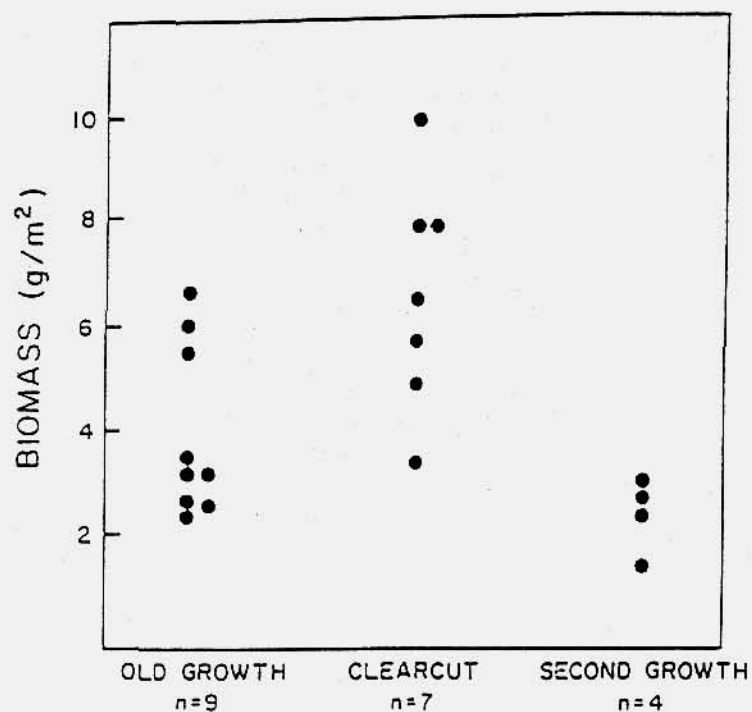
Figure 2. Trout biomass (g/m^2) in twenty streams draining old-growth, clearcut, and second growth forests of the western Cascades. From Murphy (1979)

Salmonids in downstream reaches are generally more limited by space than by food (**Chapman 1966; Hearn 1987**), but they are also known to defend feeding territories which are adjusted in size according to food availability (**Dill 1978; Dill et al. 1981; Grant and Kramer 1990**). In other words, they defend smaller territories if more food is available, and larger territories if less is available—a classic example of a density-dependent mechanism regulating population size. Projecting this to headwater stream reaches, **Sabo (1995)** has suggested that population densities and biomasses are as low as they are there because the fish are defending even larger territories due to the lower food abundance. However, as will be discussed later, **Elliott (1989)** found that density dependence plays no role in regulating the size of an isolated above-waterfall population of brown trout.

How much food is needed to sustain a headwater fish? I estimated this from data in the literature. **Weatherley and Gill (1981)** considered 3 percent of an individual fish's dry weight to be a "restricted" or "limited" diet on which 69-116 mm FL rainbow trout grew only slowly at 12° C when held under controlled conditions in the laboratory. I assumed that this value holds for fish in the wild as well, and I used information from **Elliott (1976)** that fish dry weight is about 25 percent of fish live weight. I chose fish live weights of 5g, 10g, 20g and 30g (corresponding to fish of approximately 50 to 130 mm FL) as representing the size range typically observed for trout in uppermost-fish reaches. Thus:

**Table 1. Minimum amount of food required per day
to maintain four different sizes of uppermost fish**

Fish live wt., g	Fish dry wt, g (0.25 x live wt.)	Dry wt. food needed per day, g. (0.03 x dry wt)
5	1.25	0,038
10	2.50	0.075
20	5.00	0.150
30	7.50	0.225

These food dry weight values are estimates of the amounts of food an uppermost fish of each stated size would need to consume per day, of the total amount delivered by the stream to its station, in order to persist at that site. To estimate the total amount of food the stream would need to provide in order for these amounts to be captured, one needs to estimate what proportion of the food passing the fish's position will actually be seen by the fish, i.e., the size of the fish's window relative to the pocket where the fish is holding, plus three additional probabilities: (1) the probability of a food item entering the

window being attacked, (2) the probability of an attack being successful, and (3) the probability of a successfully attacked item being ingested (**McLaughlin et al. 2000**). I first assumed (for simplicity) that the fish occupies a pocket of 1 m^2 in area. For item (1), **McLaughlin et al. (2000)** assumed a probability of 1.0 and for items (2) and (3) they estimated a combined probability of 0.42. For the proportion of food entering the window, I assumed that the fish would typically hold near the substrate and its window would be shaped roughly like a quarter-sphere in front of and above its snout with a radius equal to its attack distance. For attack distance, I used 0.6 m, a value published by **Dunbrack and Dill (1983)** for salmonids in the 60-80 mm size range. Since the resulting surface area of 1.13 m^2 is larger than the 1 m^2 area assumed above for the fish's location, I assumed that the fish would see and attack all food items entering this 1 m^2 area. Therefore, the uppermost fish could be expected to consume 1.0 x 1.0 x 0.42 = 0.42, or about 42 percent of the total food delivered by the stream to its location.

Applying this percentage to the food consumption values in Table 1 gives values for total food delivered of 0.09 g dry wt. food per day; 0.18 g dry wt. food per day; 0.36 g dry wt. food per day; and 0.54 g dry wt. food per day for the four sizes of trout respectively. These are ballpark figures for the quantity of food the stream must produce per day at the uppermost-fish site (over and above the amount consumed by other predators such as larval salamanders that may be present upstream) in order for the fish living there to persist. The next chapter takes up the question of how large the stream must be, in terms of water flows, to produce a food web that just encompasses this range.

Sexual maturity occurs at an early age in populations of fish occurring at or near the upper extent of fish distribution, and this is also true generally of populations isolated above barriers such as waterfalls, even if they are not the uppermost fish (**Wyatt 1959; Blackett 1973; Jonsson and Sandlund 1979; Parkinson et al. 1984; Northcote and Hartman 1988**). Also, fish in such populations have short life spans. With regard to age, **Wyatt (1959)** reported that over 95 percent of the headwater cutthroat trout present in his study streams in Oregon's Cascade Range were in the YOY to age 3 range. The remainder, less than 5 percent, were age 4, with the exception of just a single individual that had attained the age of 5. The study of **Northcote and Hartman (1988)** generally echoed these findings for above-waterfall populations of rainbow trout and coastal cutthroat trout in British Columbia streams, and **Jonsson and Sandlund (1979 and references cited therein)** reported similar results for isolated stocks of European brown trout. **Blackett (1973)** reported that Dolly Varden charr in a resident population isolated in a small stream above an impassible falls attained sexual maturity a year earlier in life and at a much smaller size than did anadromous Dolly Varden in two nearby southeastern Alaska streams.

Fecundity is low as well in such populations, with the number of eggs per female usually falling in the 50 to 250 range and rarely exceeding 300 eggs per female (**Blackett 1973; Nicholas 1978; Tsao 1979; Northcote and Hartman 1988; Elliott 1989**) (**Figure 3**). However, an interesting aspect of fecundity of headwater-resident salmonids is that headwater females often retain a relatively large egg size compared to their body size (**Blackett 1973; Watson 1993; B. Fransen, Weyerhaeuser Company, personal communication 2000; personal observations by author**), and may produce approximately the same number of eggs per gram of body weight as their migratory conspecifics. **Blackett (1973)** found this to be so for an isolated population of Dolly Varden charr compared with two nearby anadromous populations in southeastern Alaska. In the resident population, fecundity averaged 66 eggs per female compared with1888 eggs per female for each of the two anadromous populations. But the average egg size of 3.6 mm diameter in resident females overlapped the range for the anadromous females, as did the number of eggs per gram of female body weight. Larger egg size generally confers a survival advantage to alevins in other salmonid populations (**Bams 1969; Fowler 1972; Wallace and Aasjord 1984; Beacham and Murray 1990**). If this holds true for headwater populations as well, it means that headwater females pack a great deal of alevin-survival potential into their eggs relative to their small body size.

As noted above, headwater trout seldom live longer than about 3 or 4 years. However, the early onset of sexual maturity gives them the opportunity to spawn more than once in their lifetimes. **Elliott (1989)** considered this to be a selective advantage for trout living in above-barrier and headwater reaches. In addition, headwater and above-barrier trout often ripen, spawn, and emerge later in the year than their below-barrier counterparts (**Jonsson and Sandlund 1979; Northcote and Hartman 1988**). It has been suggested that this timing sequence may be an adaptation to flow regimes that do not settle down until later in the summer, or to the generally colder water temperatures in headwater reaches compared to downstream reaches (**Northcote and Hartman 1988; Kondolf et al. 1991**).

Average population densities of salmonids living in headwater reaches or above impassable barriers are much lower—often 5 to 100 times lower—than population densities in more favorable downstream reaches (**Northcote and Hartmann 1988**). In such low-density populations, population density and survival may not be governed by density-dependent factors as is characteristic of downstream populations. **Elliott (1989)** found this to be the case for a low-density population of brown trout isolated above a waterfall in Wilfin Beck, a small stream in England's Lake District. In this Wilfin Beck population, plots of number of survivors at different stages of the life cycle vs. parent stock size yielded straight lines, indicative of density-independent factors governing survival. In contrast, these same relationships for a population of migratory brown trout rearing at much higher density in the more favorable stream environs of nearby Black Brows Beck followed a series of dome-shaped Ricker

Figure 3
Fecundity–Fork Length Relationship for some
Headwater-Resident Coastal Cutthroat Trout
Data from Nicholas (1978) and Northcote and Hartman (1988)

$y = 1.0264x - 51.116$
$R^2 = 0.607$
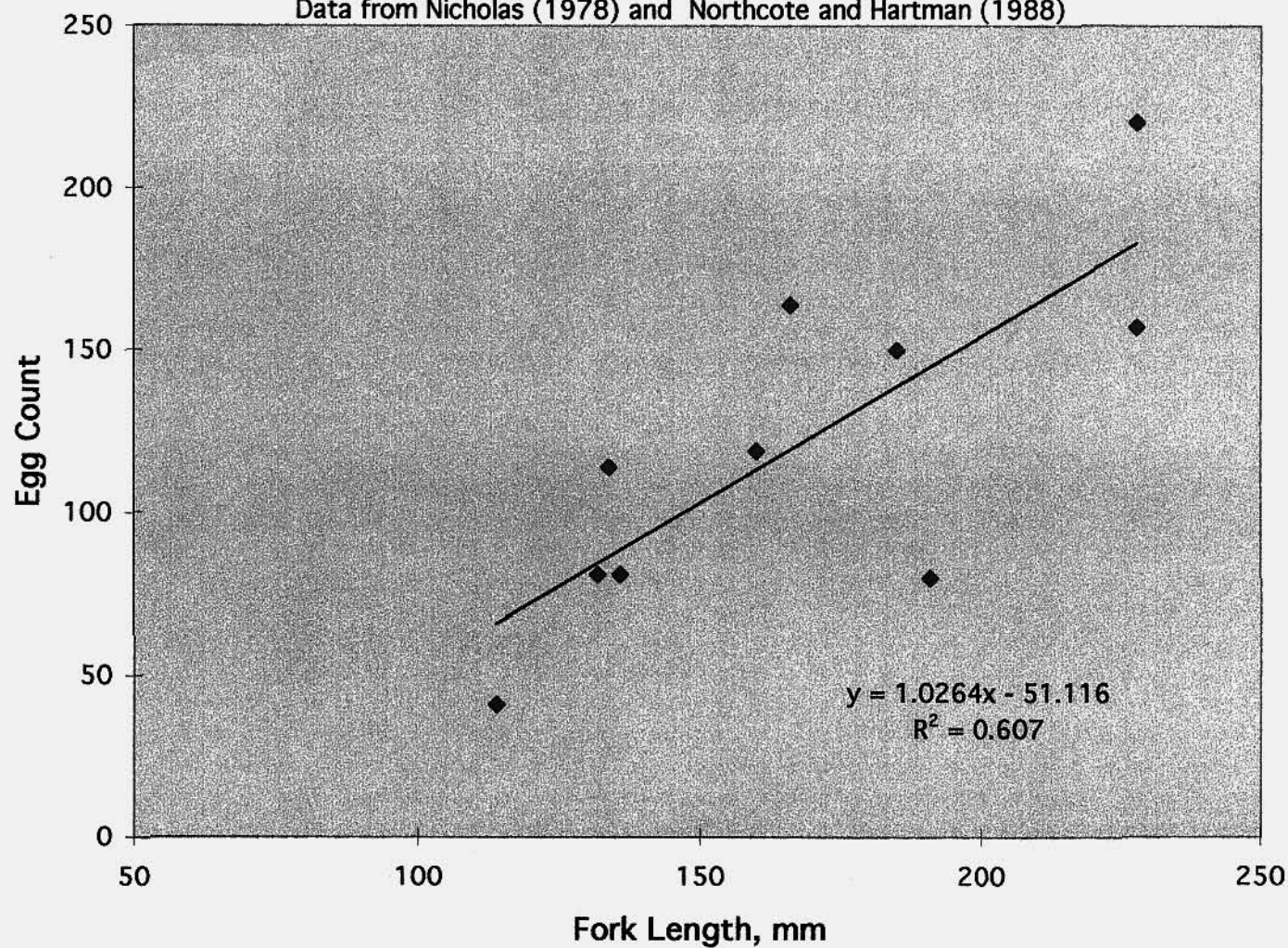
curves, indicative of a population regulated by density-dependent survival (see **Ricker 1954; also Elliott 1994**). When the data for the above-waterfall Wilfin Beck population were plotted together with the Black Brows Beck data on the latter's Ricker curve set, the Wilfins Beck data fell on the first ascending straight-line portion of each curve where the parent-recruitment relationship is near-linear and independent of density (**Elliott 1989, 1994**).

In **Elliott's (1989)** case study, trout in the above-waterfall Wilfin Beck population exhibited little movement, and losses were due entirely to mortality rather than migration. Many other investigators have reported only limited movement or migration, if any at all, in headwater trout populations (**Miller 1957; Wyatt 1959; Northcote and Hartman 1988; Nakano et al. 1990; Heggenes et al. 1991; Young 1998**). This is not to say that such fish are sedentary under all conditions, however. In fact, the limited-movement paradigm has been challenged recently by investigators who have found that trout in high elevation streams of Colorado and Wyoming appear to be much more mobile and move far greater distances over the full course of a year than previously believed (**Riley et al. 1992; Gowan et al. 1994; Gowan and Fausch 1996**). On the other hand, the higher in the headwaters these trout are found, the more limited their movements seem to become (**Young 1998**). Perhaps it is best to just say that it may be important to maintain stream connectivity even in headwater reaches so that the trout may exercise free movement to access whatever habitats they need to fulfill their spawning, rearing, and overwintering requirements. Even the uppermost fish in a stream must have sufficient mobility to find a mate in order for its population to persist.

Adaptive Genetic Uniqueness of Above-Barrier and Uppermost Trout Populations

Elliott (1994) pointed out that trout populations existing above and below waterfalls provide some of the best examples of divergence between neighboring populations. Losses due to migration would seem to be detrimental to uppermost fish populations, especially so for those living above natural barriers to upstream movement. Fish passing downstream over the lip of the barrier would be lost from the upstream gene pool, thereby setting up a stringent one-way barrier to gene flow. **Northcote and Hartman (1988)** called this *knife-edge selection*. **Elliott (1994)**, citing one of Haldane's hypotheses (**Haldane 1956**), proposed that this kind of stringent knife-edge selection would favor those genotypes adapted to density-dependent factors in favorable habitats that allow for high population densities. But only those genotypes most adapted to density-*independent* factors would be selected in less favorable habitats that allow for only low population densities. The latter populations often occur at the edge of a species' range, and trout populations living above waterfalls and at the upper end of their distribution in streams also fall into this category. For theoretical genetic models (and a highly mathematical

treatment) of how populations can persist in such places where population densities approach very low levels, see **Asmussen (1979)**.

Small body size, early maturation, short life span—and, although not mentioned in the earlier discussion, retention of juvenile fin and body form and juvenile coloration (i.e., retention of parr marks) throughout maturity in some populations—are characteristics typically exhibited by above-barrier and uppermost fishes. These have been called "juvenilization" characters, and the suggestion has been made that they are responses to long isolation or insularization. Body size reduction, for example, is analogous to island populations of mammals, where records available since the Pleistocene indicate that body size reduction has been a common response to suboptimal habitat conditions **(Heaney 1978)**. **Riddell and Leggett (1981)** demonstrated that there is a general relationship between flow regime and body morphology in juvenile Atlantic salmon, such that fish rearing in streams with swifter currents have more fusiform bodies and longer paired fins than their counterparts rearing in slower streams. **Elliott (1989)** considered early maturation and the opportunity to spawn more than once in their lifetimes despite their short life spans to be selective advantages for trout living in headwater and above-barrier stream environments. Large egg size relative to female body size (and the attendant high potential for alevin survival) would be another such advantage.

It was noted earlier that above-barrier and headwater trout often ripen, spawn, and emerge later in the year than their below-barrier downstream counterparts **(Jonsson and Sandlund 1979; Northcote and Hartman 1988)**. This particular timing sequence may be an adaptation to flow regimes that do not settle down until later in the summer, or to the generally colder water temperatures in headwater reaches compared to downstream reaches **(Northcote and Hartman 1988; Kondolf et al. 1991)**.

Many investigators have now reported distinct genetic differences between above-barrier and below-barrier trout populations **(Northcote et al. 1970; Jonsson 1982; Parkinson et al. 1984; Ferguson 1989; Currens et al. 1990; Hindar et al. 1991; Marshall et al. 1992; S. Phelps, Washington Department of Fish and Wildlife, personal communication 1994; Griswold 1996)**, and for at least one of these differences the adaptive significance has been worked out. **Northcote et al. (1970)** first reported that rainbow trout from above and below a waterfall on Kokanee Creek, B. C. exhibited differences both in meristic characters and in lactate dehydrogenase (*Ldh*) genotype. The above-falls *Ldh* isozyme was subsequently found to be more efficient in lactic acid conversion than the below-falls isozyme, thereby conferring greater swimming stamina to the above-falls trout **(Tsuyuki and Williscroft 1973, 1977)**. In laboratory studies, juvenile rainbow trout homozygous for the above-falls form of *Ldh* showed a more positive response to water current (i.e., greater upstream movement against the current) than trout homozygous for the below-falls *Ldh* form (which tended to move downstream

with the current) (**Northcote and Kelso 1981**). Greater swimming stamina and positive current response are just the sorts of traits that would be selected for under knife-edge selection, and would confer advantage to fish living in above-falls stream reaches (**Northcote and Hartman 1988**).

The question is invariably asked, where an impassable barrier such as a high waterfall exists (see for example **Figure 4**) but trout are found above it and no stocking has ever taken place, how did those trout get there? A falls or steep section of channel may indeed prevent upstream migration of fish, but that does not mean the upstream reaches are barren. Most likely, their ancestors gained access at some point back in the pre- history of the area when the barrier to upstream colonization did not exist (**Currens et al. 1990**).[7] Fish populations may have become established hundreds, thousands, or tens of thousands of years ago, prior to formation of these barriers, and may persist in upstream reaches. **Elliott (1994)** pointed out that many European brown trout populations isolated above waterfalls possess the *Ldh5*(100) allele, which is considered to be the ancestral form in *Salmo trutta* (**Ferguson 1989; Hamilton et al. 1989; Marshall et al. 1992**). This allele has subsequently been replaced in most below-barrier brown trout stocks by invasions of more recently evolved fish with the *Ldh5*(90) allele. Thus, the original colonization of the isolated upstream reaches must have occurred before the present barriers became barriers.

Summary

- In Washington streams, the uppermost fish species in the stream is almost always a resident salmonid. Native cutthroat trout comprise the majority of observations, but native rainbow trout and non-native brook trout are also found. Bull trout have not been reported by Washington stream typers, but they do occur elsewhere as the uppermost fish under certain conditions. Even in streams that head up within the anadromous zone, anadromous salmonids have been observed only occasionally as the uppermost fish.

- Sculpin occur only rarely as the uppermost fish beyond the last salmonid, but do co-occur with salmonids at headwater sites. Lampreys and three-spine sticklebacks have been reported once each at uppermost fish sites.

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[7] In the case of Multnomah Falls, shown in Figure 4, for a period of time during the Pleistocene the Columbia River was hundreds of feet deeper through the Columbia Gorge than it is at present. Indeed, the river was deep enough to have pushed a lake up the Willamette Valley in Oregon as far upstream as Eugene. During this time, the Columbia overtopped Multnomah Falls as well as the other spectacular waterfalls in the gorge. It is likely that trout gained access to the upper creeks during this period.
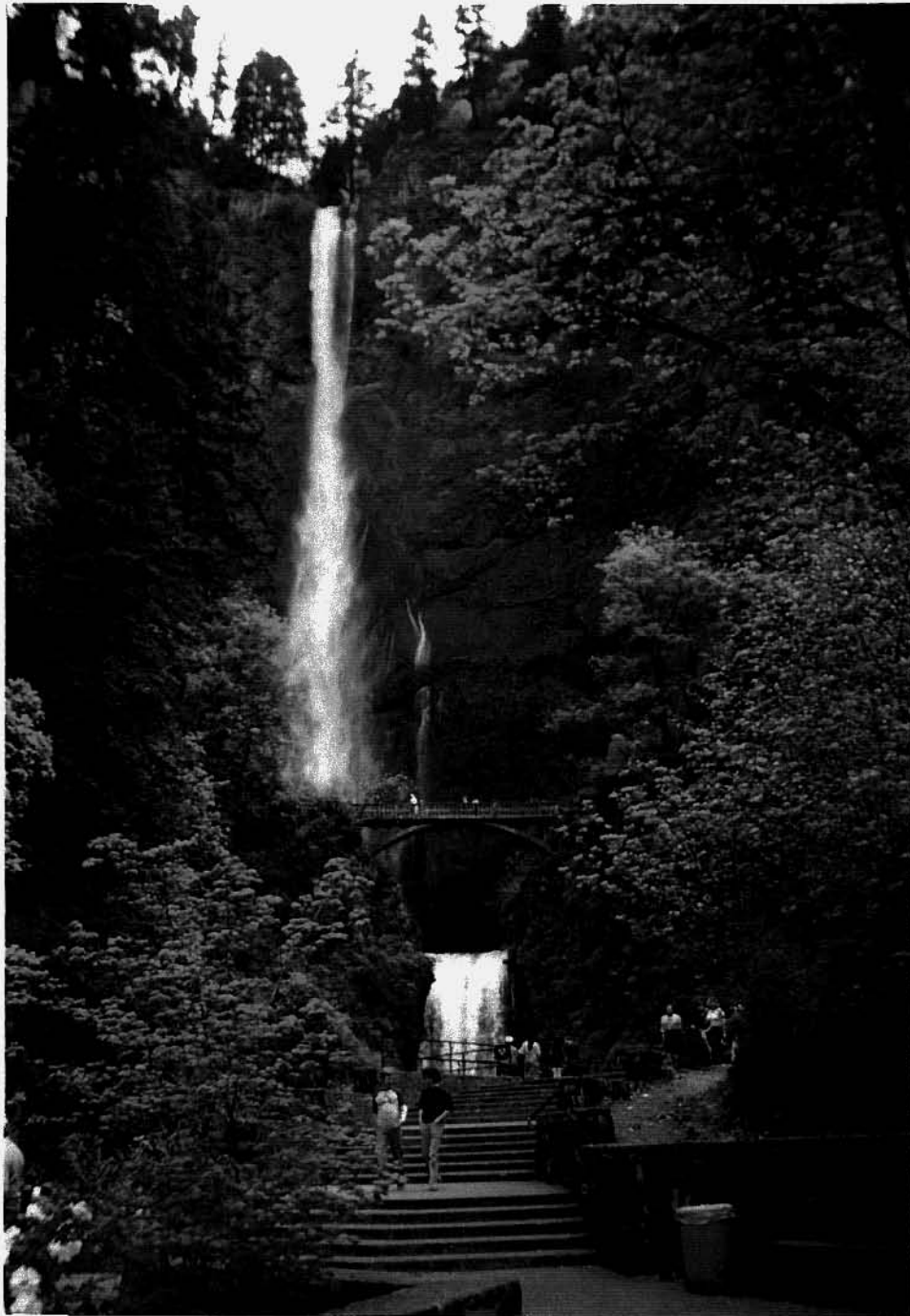
Figure 4. Multnomah Falls in the Columbia River gorge, Oregon. The creek above this high, impassable waterfall has a population of adfluvial trout, but has never been stocked.

- Stream-dwelling amphibians frequently inhabit streams above the upper extent of fish distribution, and some species may thrive in the absence of fish. On the other hand, predation on small salmonids and the pressure of competition for scarce food resources have been suggested as factors limiting upstream distribution of fish.

- Small body size, retention of juvenile body form and skin coloration throughout maturity, early maturation, low fecundity, and short life span relative to their downstream counterparts are characteristics of headwater and above-barrier salmonids. These "juvenilization" traits have been called responses to isolation or insularization and may confer selective advantage on salmonids living in headwater and above-barrier stream environments.

- Evidence suggests that survival and growth of headwater and above-barrier trout may be governed by density-independent factors, as opposed to density-dependent factors governing the population dynamics of downstream populations.

- Owing to "knife-edge selection," genotypes resistant to downstream migration along with genotypes adapted to density-independent factors may dominate in headwater and above-barrier populations.

Chapter Three—The Nature of Habitat, and Fish Utilization of Habitat, at the Upper Extent of Distribution

Uppermost-Fish Reaches in Context—Stream Size in Terms of Water Flow and Basin Area

In Chapter Two, an estimate was made of how much food would have to be provided by a stream to sustain an uppermost fish. Here we ask, how large must a headwater stream channel become, i.e., how much water must it be carrying, in order to produce that level of a food web? Assuming that a fish must find *both* food and habitat[8] in order to persist at the upper bound of distribution, we can also ask, how much water does the channel have to be carrying before it can produce habitat features *suitable for* the uppermost fish?

Fransen et al. (1998) obtained data that provides at least a provisional answer to both questions. In a survey of 79 southwestern Washington streams where they field-verified uppermost-fish locations, **Fransen et al. (1998)** also estimated mean annual flow rates at the upper bound of fish distribution. As shown in **Figure 5**, 90 percent of these streams had mean annual flows of 3.5 cfs (0.1 m³/sec.) or less at the upper bound; 80 percent had mean annual flows of 2 cfs (0.06 m³/sec.) or less at the upper bound; 65 percent had mean annual flows of 1 cfs (0.03 m³/sec.) or less at the upper bound; and somewhat fewer than 25 percent of the sites had mean annual flows of 0.5 cfs (0.01 m³/sec.) or less. The distribution of flow rates is left-skewed, with a fairly sharp peak at around 1 cfs (0.03 m³/sec.) or a bit less. One can conclude, then, that where these streams attain enough water to provide a mean annual flow of 1 cfs (0.03 m³/sec.), with a range from, say, 0.5 to 3.5 cfs (0.01 to 0.1 m³/sec), they have the potential to produce a minimum fish-sustaining food web. Otherwise, **Fransen et al. (1998)** would not have found fish there.

Before continuing, it needs to be made clear that there is wide variation in the capacity of stream systems to generate food **(Bisson and Bilby 1998)**. Some important factors involved include (1) the underlying bedrock and the effect it has on nutrient availability; (2) light levels impinging on the stream; (3) type and amount of riparian vegetation; and (4) inputs of food from the surrounding terrestrial landscape. The spread of the data in Figure 5 may illustrate this variation for the 79 streams included in

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[8] There is one potential exception to this food and habitat paradigm. Occasional observations have been made of anadromous salmonids spawning at the very heads of spring creeks, areas which are typically lacking in adequate summer rearing habitat **(M. Ereth, Skokomish Tribe, personal communication 2000)**. In these situations, since emergent fry must move downstream anyway, food may no be so important. The main consideration may be sufficient stream power to create and maintain adequate spawning and incubation habitat. Spring creeks need more research attention in this context.
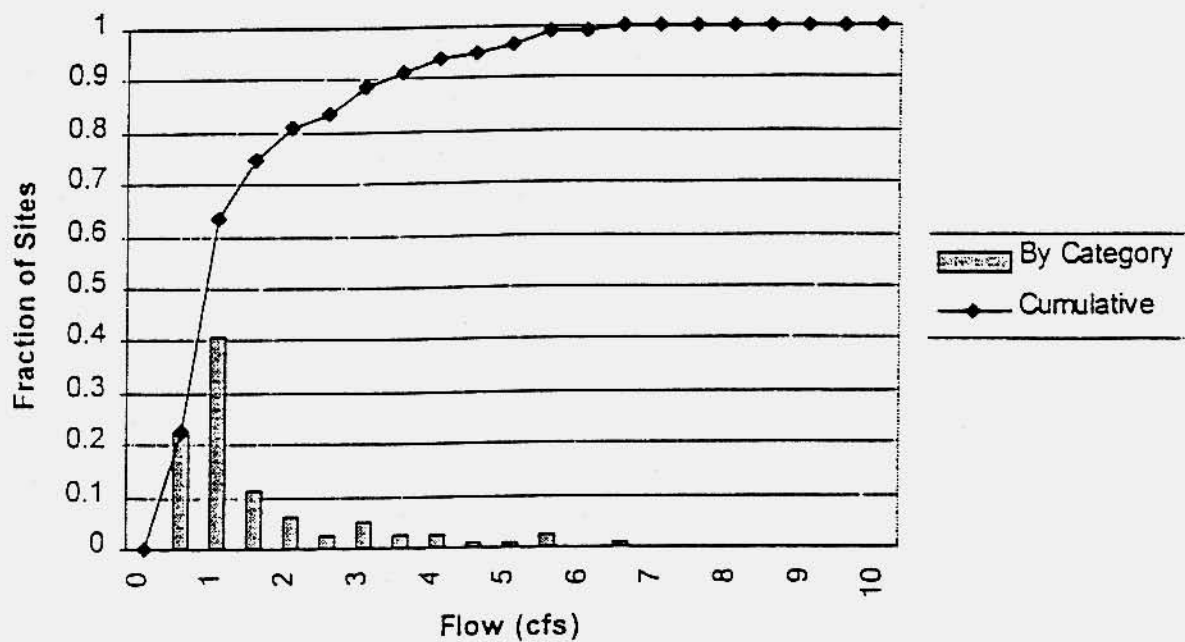
Figure 5. Mean annual flows at fish bearing water boundaries for 79 streams in the western Cascade foothills and Willapa Hills. Estimates derived from basin area and average annual precipitation calculations. From Fransen et al. (1998).

the **Fransen et al. (1998)** study. These data do provide us with a rule-of-thumb, or mental picture if you will, of the size of stream needed to allow a fish to persist, but this hypothesis needs further testing by field work, especially in other ecoregions of the state.

That same mean annual flow rate, i.e., 1 cfs (0.03 m^3/sec.) or a bit less with a range from, say, 0.5 to 3.5 cfs (0.01 to 0.1 m^3/sec), applies to the question of habitat creation as well. Again this follows *a priori* from the fact that uppermost fish locations verified by **Fransen et al. (1998)** fell within this range. If one accepts that the habitat-creating work of a channel is done at bankful flow (**Andrews 1980; Leopold 1994**), and using an extrapolation from charts in **Leopold (1994)** that bankful flow is about 11 times mean annual flow for this region, then channels capable of carrying bankful flows of about 11 cfs (0.31 m^3/sec) with a range between 5.5 and 38.5 cfs (0.16 and 1.09 m^3/sec) could generate sufficient stream power to create habitat features suitable for fish. But yet again, this is a hypothesis that needs further testing in other ecoregions of the state.

How much drainage area is required to put a mean annual flow of 1 cfs (0.03 m^3/sec.) in the channel? The answer to this question is, it depends on where in the region the channel is located. To put this in context, consider the following simple word-picture, which is also illustrated in **Figure 6**.

When precipitation falls at the top of a catchment and runoff occurs, it takes a certain amount of drainage area just to accumulate enough water to form a channel (**Montgomery and Dietrich 1988, 1989**). This is the channel initiation point, or *channel head* as it is labeled in Figure 6. Runoff from an additional amount of drainage area is then required for the fledgling stream to accumulate the nutrients needed to build a food web capable of supporting a salmonid, and to develop enough power to create suitable habitat. This is labeled *threshold of fish use* in Figure 6. Salmonid fishes will never be found above this point in the stream, because there is simply not enough of one or the other or both key resources to sustain them. This is the intrinsic upper limit of fish habitation.

But the amount of drainage area required to initiate a channel—and, in turn, to achieve the fish-sustaining threshold—is not the same for all basins. It varies with the climate, geology, and topography of the basin, i.e., the basin's geomorphic province (**Montgomery 1999**) or ecoregion. For Washington streams, the Forest Practices Emergency Rules apply these presumed basin sizes for perennial flow initiation as default values for determining Type 4/5 water boundaries:[9]

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[9] Reviewers of this report point out that these numbers are provisional and will be validated over the next few years using a larger sample and consistent field protocol. The 300-acre value for eastern Washington is especially suspect, since it takes only 175 acres of basin area to have a presumed fish-bearing stream in eastern Washington under some conditions (**T. Jackson, Washington Department of Fish and Wildlife, personal communication 2000**).
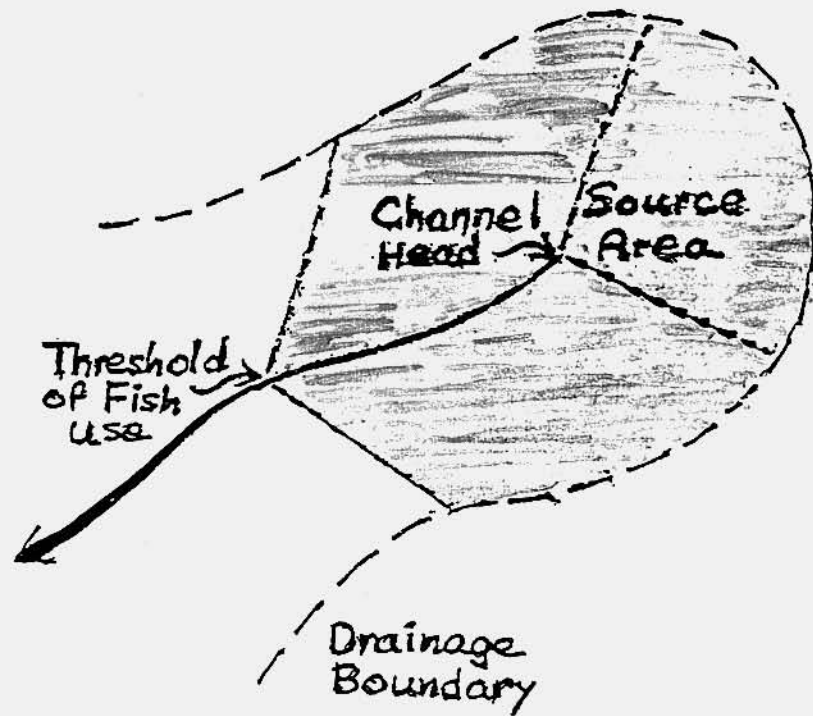
Figure 6. Relation between source area, threshold of fish use, and the related first-order basin. After Montgomery and Dietrich (1989).

Coastal area, Sitka Spruce Zone	13 acres (5.3 ha)
Rest of western Washington	52 acres (21 ha)
Eastern Washington	300 acres (121.4 ha)

Work done in the early 1990s by the Oregon Department of Forestry (**Lorensen et al. 1993**) and additional work done more recently here in Washington as part of the reformulation of Forest Practices Rules further demonstrates the geomorphic province or ecoregion effect. Some of the data from Oregon are shown in **Figure 7**. To obtain these data, Oregon Department of Forestry personnel identified the upper extent of fish presence in streams in eight townships, each in a different geomorphic province of the state. They then determined the basin area draining to that point for each stream, and cumulative plots were made to show proportion of sites with fish vs. basin area. Results for four of the eight townships, representing four western Oregon ecoregions, indicate that there is little difference between the central and north coast ecoregions, nor between the south coast and Siskiyou ecoregions. But a considerable difference exists between the two pairs of ecoregions. For the central and north coast ecoregions, it takes about 80 acres (32.4 ha) of drainage area for a 50 percent probability of fish presence in a stream. But in the south coast and Siskiyou ecoregions, where both geology and climate are abruptly different, about 300 (121.4 ha) acres of drainage area are required for a 50 percent probability of fish presence.

Reach Descriptions using Stream Classification

The discussion above was intended to provide a contextual picture of uppermost-fish locations in terms of stream size and the size of the drainage area needed to achieve that size in different settings. For further context, let us now consider how uppermost-fish reaches would be described using stream classification methodologies.

Much has been written about how to classify rivers and streams using similarities of form and function (**Montgomery and Buffington 1998; Naiman 1998**). Classification methods currently in vogue are based on a hierarchical approach (**Frissell et al. 1986**) that links large, region-scale processes with small, microhabitat-scale processes. We have already talked some about the geomorphic province or ecoregion level. Progressing further down the hierarchy, methods enjoying use in the Pacific northwest include **Cupp's (1989a, b, 1990)** valley segment typing system; **Rosgen's (1994; 1996)** system for classifying stream segments; **Montgomery and Buffington's (1993, 1997, 1998)** system for stream reach classification; and the **Hawkins et al. (1993)** modification of the channel unit classification
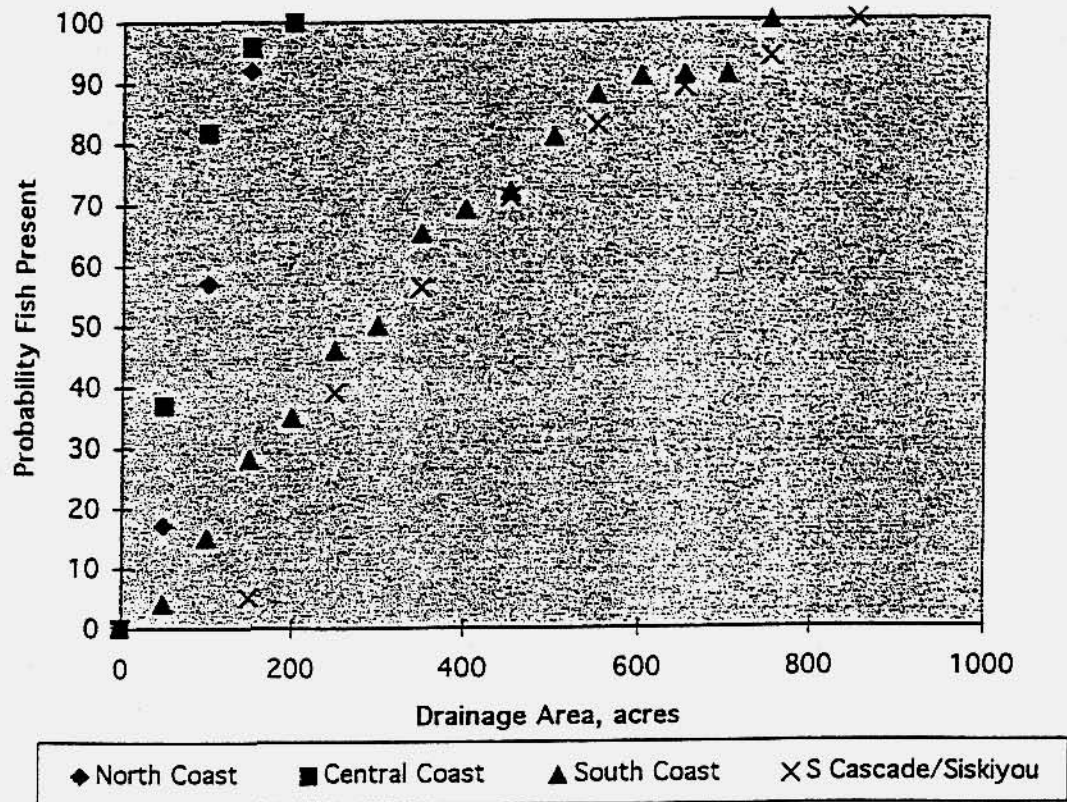
Figure 7. Probability of fish presence as a function of drainage area for streams in four Oregon ecoregions. Data from Lorensen et al. (1993).

system of **Bisson et al. (1982).**[10] It is left to the reader to sort out and assimilate the details of these methods from the original references. The purpose here is to use them to gain a sense of the settings where most uppermost-fish reaches are located in Washington watersheds and how these reaches would be described in terms of the hierarchy of landform and geomorphic characteristics in which they are found.

One feature shared among the classification systems of **Cupp (1989a, b, 1990), Rosgen (1994, 1996),** and **Montgomery and Buffington (1993, 1997, 1998)** is at least some mention of overall channel gradient in the descriptions of categories. Often, in using these systems, overall channel gradient is measured from a map, the 1: 24,000 USGS quadrangle being a commonly employed scale. Or, gradient may be determined in the field, for example, by averaging readings taken at evenly spaced intervals along a 100 m length of stream. From Chapter One, Washington stream typers have found fish in stream segments with gradients as steep as 31 and 35 percent using the latter method (**S. Conroy, Washington Trout, personal communication 1996; J. Silver, Hoh Indian Tribe, personal communication 1996**)—although **Light (1997),** in compiling fish presence-absence data from a broader stream typing data set, pointed out that fish occurrences in segments steeper than15 percent were infrequent, amounting to only about 10 percent of the reports. It also appeared from this data set that few or no last-fish locations occurred in reaches of less than 3 percent gradient. In other words, where stream typers worked upstream through fish-bearing waters up to and beyond the last-fish location, per the standard protocol, the majority of uppermost-fish reaches were in the 3 to 15 percent gradient range, but the entire array of reported locations encompassed the range from 3 to 35 percent.

This range of channel steepness values for uppermost-fish locations in Washington is in good agreement with reports from elsewhere in the western U. S. For example, **Fausch (1989)** and **Andrus (1995)** found cutthroat trout in reaches with overall gradients up to 27 percent in Colorado and Oregon streams respectively. **Ziller (1992)** found uppermost bull trout in a reach that measured 22.5 percent in southern Oregon, and **Watson and Hillman's (1997)** three-state survey found bull trout in reaches with gradients up to 23 percent. **Kruse et al. (1997)** reported that Yellowstone cutthroat trout *O. c. bouvieri* in the Absaroka Mountains, Wyoming seldom occurred in streams with reach gradients greater than 10 percent, but they did find fish in at least one reach with a 17 percent gradient. And **Dunham et al. (1999)** found that stream gradients at the upstream limits of Lahontan cutthroat trout

[10] **Montgomery (1997,1999)** has recently published another hierarchical approach for elucidating the influence of geomorphic processes on aquatic ecosystems. This is based on easily mapped *lithotopo units* within geomorphic provinces, and within lithotopo units, *process domains.* This approach shows enough early promise that **Simpson Timber Company (1999)** adopted it as the basis for their recently released Habitat Conservation Plan. See **Montgomery (1997,1999)** for details.

O. c. henshawi distribution averaged 11.6 percent and ranged as high as 26.7 percent in streams of the eastern Lahontan Basin in northern Nevada and southeastern Oregon.

In the **Dunham et al. (1999)** study, upstream distribution limit was correlated not only with stream gradient, but also with maximum basin elevation. Because of the possibility of covariation between these two parameters, **Dunham et al. (1999)** suggested that upstream limits of Lahontan cutthroat trout may simply be constrained by the maximum elevation of stream basins and are actually little influenced by steep gradients. Consistent with this suggestion, results of a study just published by **Isaak and Hubert (2000)**, using a paired-reach study design, found no indication that increased stream slope alone negatively affected trout biomass in eighteen Rocky Mountain streams across Wyoming and Idaho.

But getting back to Washington streams, it appears clear that reaches containing uppermost-fish locations fall into a rather broad range of steepness, from 3 to 35 percent. In the **Cupp (1989a, b, 1990)** system of valley segment classifications, that range of steepness could place these reaches in any one of nine valley segment classes: *M1, V1, V2, V3, U2, U3, H1, H2, or H3*.[11] The *V1* (*V-Shaped Moderate Gradient Valley*) and *H3* (*Valley Wall/Headwater*) classes are illustrated in **Figure 8A**. In the **Rosgen (1994, 1996)** system, most of these uppermost-fish reaches would fall into the *A* or *Aa+* categories illustrated in **Figure 8B**, and in the **Montgomery and Buffington (1993, 1997, 1998)** system, they would fall into the *Step-pool, Cascade, Bedrock* or *Colluvial* stream reach categories. I have listed the landform, geomorphic, and other key descriptors used to characterize each of these categories in **Table 2**.

It is probably safe to remove the *Colluvial* stream reach category from this list. *Colluvial* reaches usually occur where drainage areas are just large enough to sustain a channel for the local ground slope (**Montgomery and Dietrich 1988**). By the point where the stream flow itself has become large enough to generate a food web and create salmonid-supporting microhabitat features, the reach characteristics have probably transitioned from colluvial to one of the other stream reach categories. Thus, by virtue of where they typically occur in the drainage, *Colluvial* reaches would probably be above the upper boundary of fish use. It is worth noting that steep headwater channels in mountain drainage basins may alternate through time between *Colluvial* and *Bedrock* morphologies in response to periodic scour by debris flows (**Benda 1990**).

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[11] Cupp changed letter designations for his valley segment types between the 1989 and 1990 references. The designations used here are from the 1990 reference.
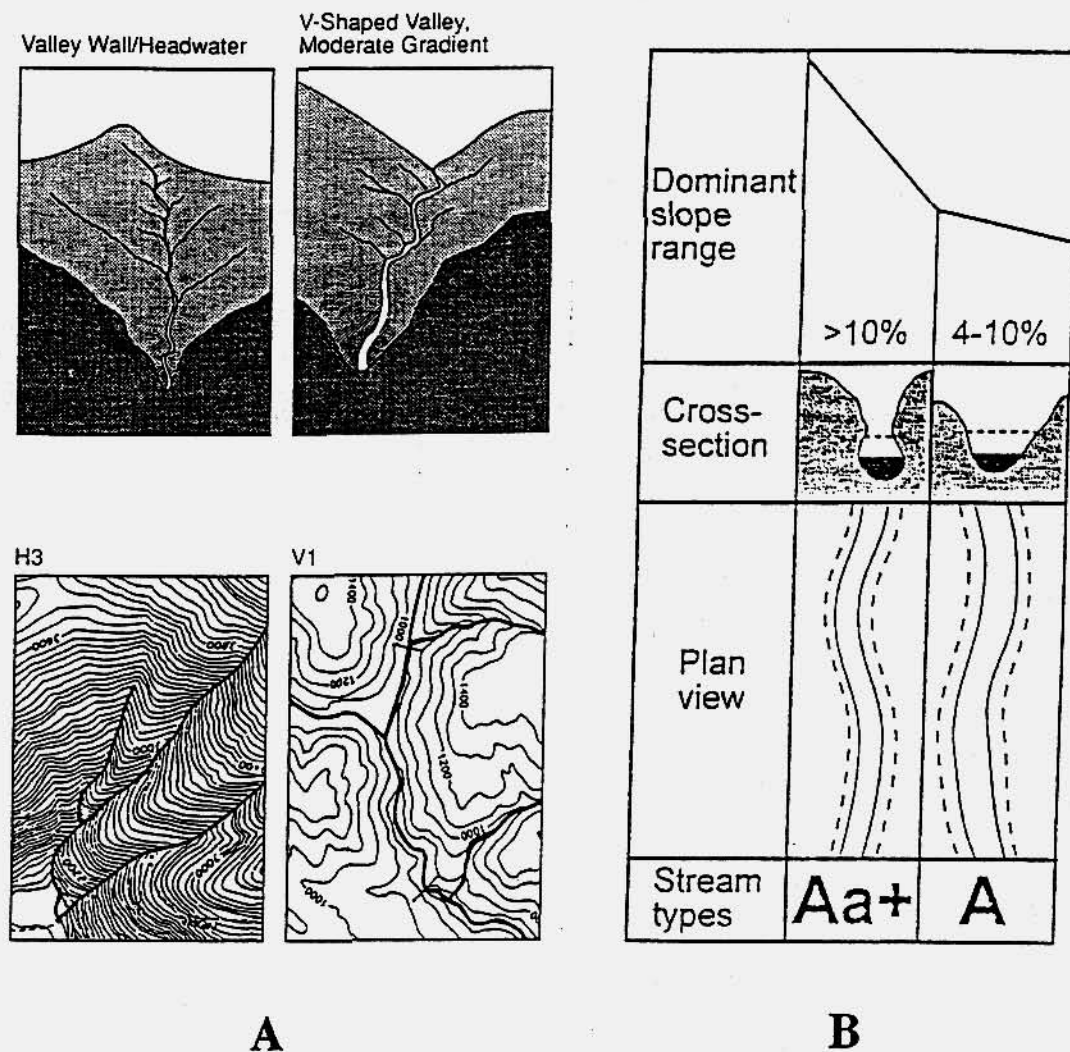
Figure 8. Schematic examples of two Cupp valley segment types (A, from Cupp 1990) and two Rosgen channel segment types (B, from Rosgen 1994) that encompass the gradient range of uppermost-fish locations in Washington

Table 2. Landform, geomorphic, and other physical characteristics of uppermost-fish reaches from commonly used stream classification systems

Valley Segment, Channel Segment, Reach Type	General Description	Landform and Geomorphic Features
M1 (Cupp)	Moderate slope bound valley segments. 2-5% gradient. Channel pattern constrained, infrequent meanders	Constrained, narrow floodplains bounded by moderate (10-30% sideslopes. Typically found in lowlands & foothills but may occur on mountain slopes and volcano flanks
V1 (Cupp) (Fig. 8A)	V-shaped moderate gradient (2-6%) valley segments. Channel pattern constrained.	Deeply incised drainage ways with steep (30-70%) competent sideslopes. Very common in uplifted mountain topography.
V2 (Cupp)	V-shaped high gradient (6-11%) valley segments. Channel pattern constrained.	Same as V1, except longitudinal valley bottom profile steep with pronounced stairstep characteristics.
V3 (Cupp)	Bedrock canyon valley segments, 6-11% valley bottom gradients. Channel pattern highly constrained.	Canyon-like stream corridors with sideslopes greater or equal to 70%. Frequent bedrock outcrops, frequently stairstepped profile. Generally associated with folded, faulted, or volcanic landforms.
U2 (Cupp)	Incised U-shaped valley segments, moderate (2-5%) valley bottom gradients. Channel pattern moderately constrained.	Channel downcuts through valley bottom glacial till, colluvium, or coarse glacio-fluvial deposits. Immediate sideslopes composed of unconsolidated, often unsorted coarse-grained deposits.
U3 (Cupp)	Incised U-shaped valley segments, high (6-11%) valley bottom gradients. Channel pattern same as U@.	Same as U-2

H1 (Cupp)	Moderate gradient (3-6%) valley wall/headwater segments. Channel pattern constrained.	Small drainage ways with channels slightly to moderately entrenched into mountain toe slopes or headwater basins. Sideslope gradients greater than 30%.
H2 (Cupp)	High gradient (6-11%) valley wall/headwater segments. Channel pattern constrained and stairstepped.	Small drainage ways with channels moderately entrenched into high gradient mountain slopes or headwater basins. Sideslopegradients greater than 30%. Bedrock exposures & outcrops common. Locallized alluvial/colluvial terrace deposition.
H3 (Cupp) (Fig. 8A)	Very high gradient (greater than 11%) valley wall/headwater segments. Channel pattern constrained and stairstepped.	Small drainage ways with channels moderately entrenched into very steep mountain slopes or headwater basins. Sideslope gradients greater than 60%. Bedrock exposures and outcrops frequent.
A (Rosgen) (Fig. 8B)	Steep (4-10%) entrenched, cascading or step-pool stream segments. High energy/debris transport where associated with depositional soils. Very stable where channels are bedrock or boulder dominated.	High relief. Erosional or bedrock forms.
Aa+ (Rosgen) (Fig. 8B)	Very steep (10% +), deeply entrenched, debris transport stream segments.	Very high relief. Erosional, bedrock, or depositional features. Debris flow potential.
Step-pool (Montgomery & Buffington)	Moderate to steep gradient (3-10%) moderately confined cobble-boulder reach, pool spacing 1-4 channel widths.	Transport reaches. Dominant sediment sources fluvial, hillslope, debris flows. Dominant roughness elements are bedforms (steps, pools), boulders, LWD & banks. Cobble/boulder are predominant bed materials.

Cascade (Montgomery & Buffington)	Steep (10-30%) strongly confined, boulder bed reaches. Pool spacing less than 1 channel width.	Transport reaches. Dominant sediment sources fluvial, hillslope, debris flows. Dominant roughness elements boulders & banks. Dominant bed materials are boulders.
Bedrock (Montgomery & Buffington)	Vairable-gradient reaches confined by valley walls. Pool spacing variable.	Transport reaches. Dominant sediment sources same as above. Dominant roughness elements bed & banks. Predominant bed material bedrock. Channels lack continuous alluvial bed but may store some alluvial materials temporarily in scour holes or behind obstructions.
Colluvial (Montgomery & Buffington)	Steep (gradients greater than 20%) strongly confined reaches with variable pool spacing.	Source reaches. Dominant sediment source debris flows. Dominant roughness elements boulders and LWD. Predominant bedform materials variable. Typically occupy the very headwaters where drainage areas are just large enough to sustain a channel.

What Table 2 says, in essence, is that upper bounds of fish use at the valley segment and stream segment levels of the stream classification hierarchy may be found well upstream in upper valley sidewall and headwall tributaries that comprise the actual headwaters of a basin, and in lower valley sidewall tributaries that may originate on steep valley walls but enter the mainstem lower down in the basin. **Sedell et al. (1982)**, who worked on ecology and habitat requirements of fish populations in the South Fork Hoh River, provided excellent word-pictures of these kinds of tributaries that are useful compliments to the stream classification descriptions, especially for field workers such as stream typers.

Uppermost-Fish Locations at the Stream Reach and Channel Unit Scales

Montgomery and Buffington's (1993, 1997, 1998) channel reach classification system is especially useful because at this level of the hierarchy we can at last begin to visualize how fish actually deploy and utilize physical habitat at and near uppermost-fish sites. At this level of the hierarchy it is also possible to make distinctions between reaches that fish can inhabit and reaches that they probably cannot. The **Montgometry and Buffington (1993, 1997, 1998)** channel reaches, and within these reaches the channel unit descriptions of **Bisson et al. (1982; see also Hawkins et al. 1993)**, are particularly useful for correlating field observations and reports.

For example, in such widely separated locales as the Rocky Mountains of Colorado (**Fausch 1989**) and the Cascade and Coast Range mountains of western Oregon (**Andrus 1995**), the steepest-gradient reaches where cutthroat trout were reported to occur were those with a stair-step or *Step-pool* morphology in the vernacular of both the **Montgometry and Buffington (1993, 1997, 1998)** and **Bisson et al. (1982)** classification systems. This matches with observations of the few Washington stream typers who have reported on these details, where the steepest occurrences of trout, in reaches of 31 and 35 percent reach gradient, were also *Step-pool* morphology (**S. Conroy, Washington Trout, personal communication 1996; J. Silver, Hoh Indian Tribe, personal communication 1996**). On the other hand, both **Fausch (1989)** and **Andrus (1995)** reported that in reaches lacking the *Step-pool* morphology, the upper gradient limit for cutthroat trout presence appeared to be about 15 percent. **Montgometry and Buffington (1993, 1997, 1998)** channel reaches and **Bisson et al. (1982)** channel units that fit this latter category are those with *Bedrock* and *Cascade* morphologies. This distinction between steep reaches and channel units that probably could and could not support trout is illustrated in **Figure 9**.

However, bedrock and cascade reaches steeper than 15 percent should not be construed as boundaries without field verification if step-pool or other suitable reaches occur above them. Nor should debris
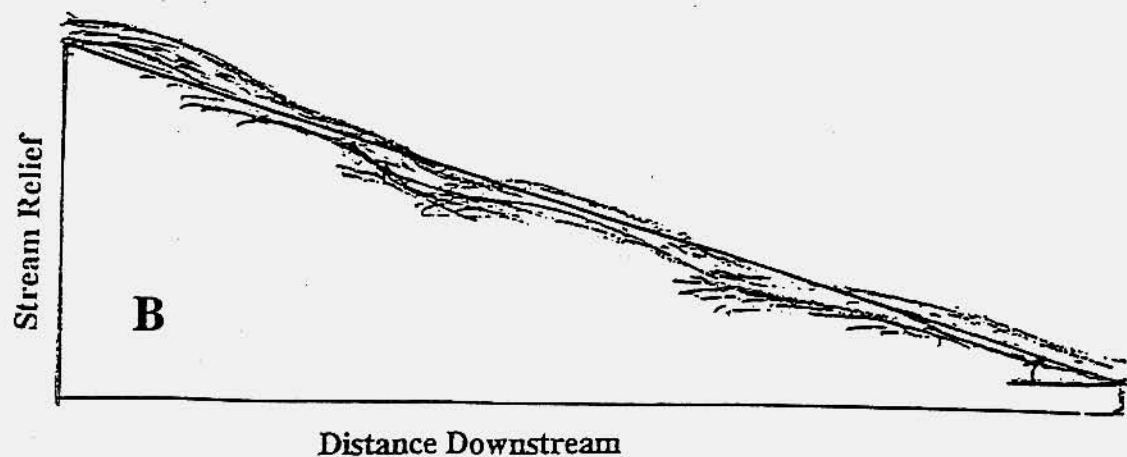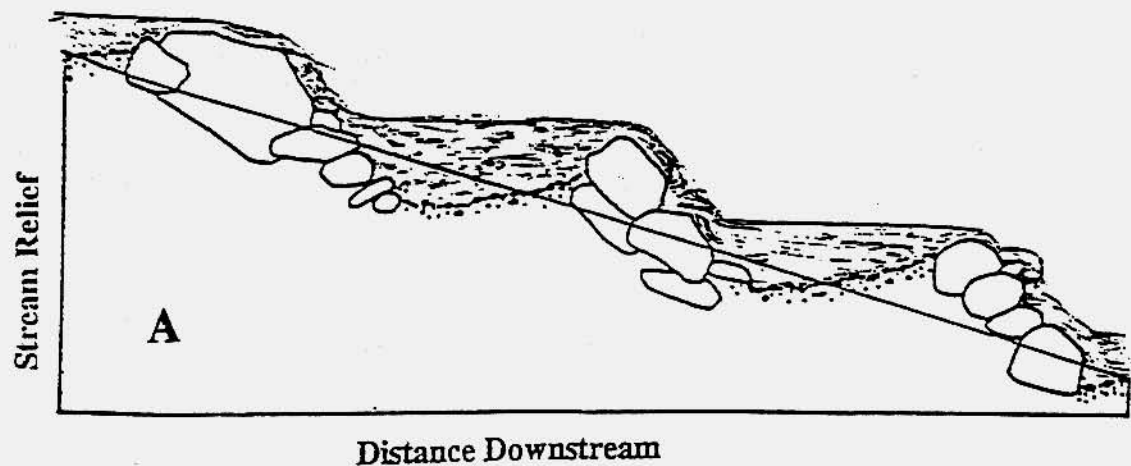
Figure 9. Longitudinal profiles of (A) a reach with step-pool morphology and (B) a reach with bedrock morphology. Overall reach gradient is 29 percent in both cases. Reach A could harbor trout in the pools and pockets at the base of the steps. Reach B, where the water surface profile is very nearly the same as the overall reach gradient, would be too steep to harbor trout.

jams that appear to block small, steep channels. In the epilog of his recent book, *Salmon Without Rivers*, **Lichatowich (1999)** wrote about watching a cutthroat trout safely ascend such a jam on a tiny, steep, headwater tributary of the Pysht River. It negotiated the "barrier" by leaping and struggling from one to another to another small puddle formed by rivulets of the stream as the water trickled down over and among the logs on the face of the jam.

In steep *Step-pool* reaches or channel units such as illustrated in **Figure 9A**, the places where trout find occupancy are, of course, the tiny pockets and pools at the base of the steps. It has been written that pools should have at least 305 mm (12 inches) of residual depth as measured by the method of **Lisle (1987)** to be optimal for cutthroat trout. Indeed, **Andrus (1995)** has advised that cutthroat trout will abandon a reach if residual pool depths drop below about 380 mm (15 inches). However, this is another of those rules-of-thumb developed in flatter *Pool-riffle* reaches further downstream and may not be such a hard-and-fast rule for trout at the upper extent of their distribution. There probably is an optimum residual pool depth for uppermost trout, but it may be geared more to the small size of the fish at these locations and to the energetics of the site than to any value extrapolated from downstream. More field work is needed to sort this out.

Figure 9 also illustrates another important point, that being that the proper measure of gradient tolerable by fish is probably not an overall reach-scale measurement, but rather gradient as measured at the channel unit or microhabitat scale. In **Figure 9**, the overall reach gradient is 29 percent for both reach morphologies. Trout could find homes in the flat pools and pockets shown in **9A**, but not anywhere in **9B**. As shown in **9A**, water surface gradients of the channel units and microhabitats where the fish actually hold are flat, probably not more than about 4 percent in most cases. Thus, gradient as taken from water surface profiles is probably the more appropriate measure of what the fish actually experience.

Microhabitat and Fish Deployment at the Upper Extent of Distribution

In the steep, step-pool reaches described above, both the habitat itself and the fish use of habitat are different from the pool-riffle reaches further downstream. For example, in streams of low to moderate gradient and well developed pool-riffle sequences (depositional reaches in the vernacular of **Montgomery and Buffington 1993, 1997, 1998**), gravels are usually relatively abundant. Spawning fish typically use sites at the pool-riffle interface (pool tailouts) or other sites where water may flow up or down through the gravel (**Smith 1941; Briggs 1953; Stuart 1954; Cope 1957; Crisp and Carling 1989; Thurow and King 1994**). But in the steep, typically boulder-bed reaches where the uppermost fish are found, pool-riffle sequences are generally absent, gravels are less abundant, and

what gravels there are occur in patterns distinctly different from lower gradient streams (**Heede 1972; Kondolf et al. 1991**). First of all, gravels that are suitable for spawning by the small-size headwater trout are themselves small, often no larger than pea-gravel size. They occur in small, isolated pockets in sites of flow divergence, most often in the lee of boulders or large wood elements; less commonly just above hydraulic controls. The water surface slopes at these locations, measured in summer when headwater trout typically spawn (**Northcote and Hartman 1988**), are much lower than the overall reach gradient and may range from only 0.4 to 4 percent or so, even where overall reach gradients may be as high as 35 percent (**Kondolf et al. 1991**).

Boulders and large wood elements serve a dual purpose in these steep, step-pool and cascade reaches. They impose the steep profile and rough bed upon the stream and thereby produce turbulent flow and high shear stress over most of the bed (**Kondolf et al. 1987**). At the same time they are effective energy dissipators and create protected sites for gravel deposition in their lee (**Heede 1972**). However, since these are transport reaches (**Montgomery and Buffington 1993**), there is likely to be a paucity of gravel in any given reach, and even the small gravel pockets that do form may be scoured in high-water events. Fish living in such reaches must have a certain amount of mobility within the reach, it would seem, in order to find suitable gravel pockets each spawning season.

The description above of the small, low-gradient pockets where spawning gravels may deposit within steeper reaches also applies to pockets where the trout find territories for summer rearing. These are the small pools at the bases of steps and cascades, and other sites of flow divergence created by boulders and large wood elements, where the slope of the water surface is much less than the overall reach gradient and water velocities are low enough to allow the fish to take up stations. The greater swimming stamina of headwater trout (**Tsuyuki and Williscroft 1973, 1977**) stands them in good stead here. As noted above, residual pool depth (**Lisle 1987**) of at least 305 mm (12 inches) is often mentioned as optimum for cutthroat trout, but this may not be such a hard-and-fast rule for the small trout of steep, headwater reaches.

Overwintering requirements of headwater trout have never been described, but two possibilities come to mind. In the first, the fish may utilize the same step-pools and flow-divergence pockets as they do in summer, provided that these sites are secure in high winter flows. In the second, the fish may move downstream to more suitable locations—given that they would not move downstream over barriers that would bar their return.

The second possibility would seem to require that headwater fish be highly mobile and adapted to flow regimes in much the same way as fish that utilize intermittent streams. A reverse analogy would apply

in the headwater-fish scenario: trout *would abandon their spawning* and summer rearing locations by moving downstream with the onset of high winter flows (or, in high elevation streams, cold winter water temperatures) then move back upstream and reoccupy these sites when winter flows recede and gravel pockets and holding stations stabilize, or as temperatures moderate. This scenario is consistent with the findings of investigators who report that trout in high elevation streams of Colorado and Wyoming may be far more mobile over the full course of a year than previously believed (**Riley et al. 1992; Gowan et al. 1994; Gowan and Fausch 1996**). These trout, it was found, move sometimes surprisingly long distances to find adequate cover for overwintering.

On the other hand, recent work by **Young (1998)** with a population of Colorado River cutthroat trout *O. clarki pleuriticus* inhabiting the very headwaters of a stream lends weight to the first possibility, i.e., the limited-movement paradigm. **Young (1998)** found that the typically small adult trout present at this site did not move to new locations and habitats as winter approached, as did the populations studied by **Riley et al. (1992)**, **Gowan et al. (1994)**, and **Gowan and Fausch (1996)**. Rather, they appeared to stay put. **Young (1998)** suggested that the small size of adult trout in his study stream may enable them to use widely available interstitial spaces beneath rubble and boulders for cover, much like juvenile salmonids (**Bjornn 1971; Rimmer et al. 1983**) or small adults (**Heggenes et al. 1983**) do elsewhere.

Other Types of Fish-Bearing Water Boundaries

Strictly speaking, the characteristics of uppermost-fish sites described above apply mainly to reaches at the steeper end of the reach gradient spectrum, and also to last-fish locations that occur somewhere along an uninterrupted segment of stream—the type called an *Along Channel* boundary in **Figure 10**. This figure was derived from a survey made by **Fransen et al. (1998)** of 306 streams in commercial timberlands of the Willapa Hills and western Cascade foothills, 80 percent of which were in reach gradients of 12 percent or less. **Fransen et al. (1998)** recognized three distinct types of of fish-bearing water boundaries in these streams:

- *At Confluence* boundaries were those where the stream typers encountered a smaller, fishless tributary entering the fish-bearing stream, but fish distribution continued in the main stream beyond the confluence. This type of boundary accounted for about two-thirds of all fish-bearing water boundaries identified in the basins surveyed.

- *Along Channel* boundaries were the next most abundant type. In reaches where these occurred, as in the steeper reaches discussed above, stream size and water flows were diminishing in an upstream direction. Sometimes streams became quite shallow with no habitat features judged by
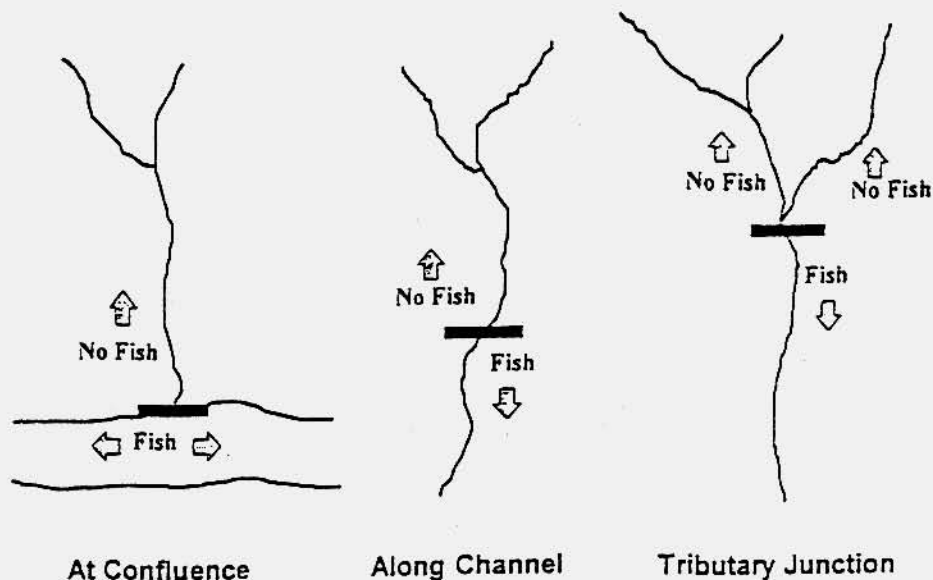
Types of Fish-Bearing Water Boundaries

Figure 10. Types of fish-bearing water boundaries observed in a survey of 306 streams in commercial timberlands of the western Cascade foothills and Willapa Hills. All boundaries were in reaches with gradients between 3 and 20 percent, but most were in reaches of 12 percent or less. From Fransen et al. (1998).

the stream typers to be suitable for fish, and in some cases flows became intermittent a short distance upstream from the field verified end of fish distribution. In other cases reach gradients became noticeably steeper upstream. But at about 10 percent of the sites, no obvious physical cause could be determined. Fish distribution simply stopped, even though habitat that the stream typers judged to be suitable appeared to be both available and accessible upstream.

- *Tributary Junction* boundaries occurred at junctions where two forks joined to produce the channel being surveyed, and neither of the two upstream forks contained fish.

With regard to the 10 percent of *Along Channel* sites where fish distribution stops for no visually apparent reason, I have personally seen many such sites in headwater streams occupied by cutthroat trout in the Rocky Mountain and Great Basin west, and so have workers from other disciplines who have published their observations.. A case in point is **Harvey (1993)** who studied aquatic insect assemblages in headwater streams with and without trout in the Wasatch Mountains of Utah. Harvey observed:

> "Sampling sites used in the comparison of streams with and without fish appeared similar physically. Daytime water temperatures varied from 10 to 20° C and did not differ between sites with and without fish. Discharge was somewhat higher at sites with fish (3.4 m^3/min [2.0 cfs] vs. 2.0 m^3/min [1.2 cfs] for sites without fish). Elevation did not differ at sites in streams with and without fish."

Harvey (1993) worked in streams with reach gradients ranging from 5 to 27.5 percent. He did not mention gradient as a factor, but did state that sites with and without fish appeared similar physically. Perhaps in this case it was merely the small difference in mean discharge that spelled the difference between fish and no fish in his study streams. In this and other cases it may simply not be worth it energetically for a fish to push upstream any further against even the most trivial impediment.

Intermittent and Ephemeral Streams

These terms are often used interchangeably, and stream scientists have alternative definitions for both. I have always felt that **Leopold and Miller's (1956)** definitions are most distinctive and I use their convention here:

- An **intermittent stream** is one in which, at low flow, dry reaches alternate with flowing ones along the stream length; or one in which the entire channel goes dry at low flow.

- An **ephemeral stream** is one which carries water only during storms.

The absence of water in stream channels often belies their importance to fish. Fish that utilize such streams move in to spawn when water is present, but are mobile enough that reconditioned adults and juveniles move out as the water recedes (**Everest 1973; Erman and Leidy 1975; Erman and Hawthorne 1976**). In the anadromous zone, **Everest (1973)** showed that many tributaries of the Rogue River, Oregon, that are often completely dry in summer, support spawning populations of steelhead in winter. The emergent fry of these steelhead remain in these tributaries for summer rearing in wet years, but in years when the streams go dry, the juvenile fish leave the tributaries for permanent streamflows elsewhere in the drainage. Also in the anadromous zone, ephemeral off-channel and terrace tributary streams are favored overwintering habitats for juvenile coho (**Cederholm and Scarlett 1981; Swales et al. 1986; Brown and Hartman 1988**). In the resident trout zone, **Erman and Hawthorne (1976)** showed that a rainbow trout population residing in Sagehen Creek, a mountain stream in California's Sierra Nevada, exhibited the same behavior as **Everest's (1973)** Rogue River steelhead. In fact, in Sagehen Creek, the trout utilized a particular intermittent tributary as their principal spawning area, even though other tributaries with permanent flow and apparently suitable spawning habitat were also available and accessible. **Erman and Leidy (1975)** found that the fry produced in this tributary were highly sensitive to the discharge regime of the stream. They remained in the tributary as long as the water level remained high, but moved downstream quickly and into the mainstem of Sagehen Creek on falling water. The amount of stranding that occurred in this situation was minimal, and this probably could be said for many if not all such natural situations.

The Washigton State Forest Practices Board uses a March 1 to July 15 time window for surveying streams to determine fish use (**Washington Forest Practices Board 2000**). In order to ensure that intermittent or ephemeral streams are surveyed when fish are most likely to be present, the Oregon Departments of Forestry and Fish & Wildlife (**Anonymous 1995**) recommend surveying them early in the period, generally between March 1 and May 31.

Summary

- Based on data from 79 field-verified fish-bearing water boundaries, stream channels large enough to carry a mean annual flow of around 1 cfs (0.03 m^3/sec) range 0.5 to 3.5 cfs (0.01 to 0.1 m^3/sec) have the potential to produce the minimum amount of food needed to sustain a fish. Streams

within this range of mean annual flows also can generate sufficient stream power to produce habitat suitable for a headwater salmonid.

- In Washington, basin area sizes of 13 acres (5.3 ha) in the coastal "Sitka spruce" zone, 52 acres (21 ha) in the rest of western Washington, and 300 acres (121 ha) in eastern Washington are the "default" values for presuming the initiation of a perennial stream under the emergency forest practice rules. If these values are correct, then somewhat larger drainage areas than these would be required to provide the key resources (food and habitat) needed to sustain a salmonid fish.

- Washington stream typers have found upprmost fish in stream segments with gradients ranging from 3 to 35 percent, although only about 10 percent of these locations are in segments steeper than15 percent.

- That range of reach gradients could place these reaches in any one of nine Cupp valley segment types, two Rosgen channel segment types, or three Montgomery and Buffington reach types. At the valley segment and channel segment levels of the stream classification hierarchy, upper-fish reaches may occur in upper valley sidewall and headwall tributaries that comprise the actual headwaters of a basin, and in upper reaches of lower valley sidewall tributaries.

- Based on field observations, the steepest uppermost-fish reaches are of the Montgomery and Buffington *Step-pool* reach type. Only this reach type has within it the types of channel units and microhabitat features that a fish could utilize in a steep-gradient reach. At reach gradients lower than 12 to 15 percent, Montgomery and Buffington *Cascade* and *Bedrock* reach types can also have habitat features headwater fish can utilize.

- The small pools and pockets utilized by fish in steep reaches themselves have water-surface gradients of 4 percent or less.

- Investigators have reported that trout in high elevation streams of the Rocky Mountain west may be far more mobile over the full course of a year than previously believed, sometimes moving surprisingly long distances downstream to find adequate cover for overwintering. However, other more recent work from the same area indicates that trout inhabiting the very headwaters of a stream exhibit only limited movements. The typically small adult trout present at uppermost sites may not move to downstream locations and habitats as winter approaches, but rather, they may take advantage of widely available interstitial spaces beneath rubble and boulders at or near their summer locations.

- In a survey of 306 streams in western Washington, 80 percent of which were in reach gradients of 12 percent or less, three distinct types of of fish-bearing water boundaries were recorded. *At Confluence* boundaries (where a smaller, fishless tributary entered the fish-bearing stream, but fish distribution continued in the main stream beyond the confluence) accounted for about two-thirds of the fish-bearing water boundaries. *Along Channel* boundaries (where stream size and water flows diminished in an upstream direction to a point where fish use ceased) were the next most abundant type. *Tributary Junction* boundaries (where two forks joined to produce the channel being surveyed but neither of the two upstream forks contained fish) was the third type.

- Regarding *At Confluence* boundaries, most of the time some abrupt change in a habitat feature was present to account for cessation of fish use; however, at about 10 percent of these sites no obvious physical cause could be determined. Fish use simply stopped, even though habitat that the stream typers judged to be suitable appeared to be both available and accessible upstream.

- The absence of water in stream channels often belies their importance to fish. Fish that utilize intermittent streams move in to spawn when water is present, but are mobile enough so that reconditioned adults and juveniles can move out as the water recedes. Where fish have adapted to intermittent water conditions, stranding may be minimal.

Chapter Four—Delineating the Upper Extent of Fish Distribution

What Determines the Upper Extent of Fish Use?

In order for a fish to persist at a given location in a stream, it needs two essential resources: physical habitat and food. If *either* is lacking, the fish cannot persist there. From the published studies and observations reviewed in Chapters Two and Three, it appears that fish use of Washington streams can start at a point where the stream is large enough to carry a mean annual flow of about 1 cfs (0.03 m³/sec), range 0.5 to 3.5 cfs (0.01 to 0.1 m³/sec). Streams within this size range appear to have the potential to produce enough food to sustain a fish (albeit not enough to grow a large fish), and can also generate sufficient stream power to produce suitable habitat (remembering that habitat suitable for a headwater fish may not be what is projected from studies of downstream populations).

How large an upstream drainage area is required to generate this 1 cfs (0.03 m³/sec) of mean annual flow? That depends on the ecoregion in which the site is located, as was illustrated in Figure 7, Chapter Three. In Washington, subject to the provisos mentioned in Chapter Three, basin areas of somewhere on the order of 13 acres (5.3 ha) are required to initiate a perennial stream in the coastal "Sitka spruce" zone of the state; somewhere on the order of 52 acres (21 ha) are required in the rest of western Washington; and somewhere on the order of 300 acres (121 ha) are required in eastern Washington. If these are the basin sizes needed just to initiate the channel, then somewhat larger drainage areas would be needed for the flow to increase to the mean annual level of 1 cfs (0.03 m³/sec).

Morphology at the reach scale of the stream classification hierarchy also appears to be an important factor governing upstream extent of fish use. As also noted in Chapter Three, fish can use steeper-gradient reaches with *Step-pool* morphology than they can reaches with *Bedrock* or *Cascade* morphologies. Examination of sites that fish actually occupy in step-pool reaches indicates that the water surface gradient of these pockets is generally always 4 percent or less even in reaches with overall gradients as steep as 31 or 35 percent.

Several additional factors, not discussed earlier, may also come into play in determining how far upstream fish presence will actually occur. The first of these is the natural fluctuation that occurs in fish populations whether human influence is present or not. Fish populations are dynamic and may fluctuate considerably even under stable habitat conditions, and these fluctuations can occur over relatively short periods of time (**Platts and Nelson 1988; Milner et al. 1993; Bisson et al. 1994; House 1995**). Four-fold to six-fold differences in fish densities from one year to the next have been

reported for populations of resident cutthroat trout in Pacific northwest streams (**Bisson et al. 1994; House 1995**). As a result, one might expect that during periods of high abundance fish would push upstream to occupy all available habitats, even marginal ones, provided that the food web would still support them, right up to the intrinsic upper threshold identified in Figure 6, chapter 3. Likewise, in periods of low abundance fish would be expected to use only sites—presumably further downstream—where habitat and food conditions may be more bountiful. In other words, one might expect the upper limit of fish distribution to be a moving point (but never above the intrinsic upper threshold!) rather than one fixed in space and time.

However, this may be another of those inferences projected from downstream observations that does not apply to fishes in headwater or isolated locations. For movement to occur in the manner described, the population would have to be governed by density-dependent factors with genotypes selected for movement in response to resource limitation or largesse. But evidence reviewed in Chapter Two indicates that populations at headwaters and those isolated above impassable barriers are governed by density-independent factors, with genotypes selected against movement. Therefore, to the extent that such movement does occur, it probably actually involves fishes downstream of the uppermost fish, and may not play that much of a role in delineating the upper extend of fish distribution in a stream. More long-term studies of this point are in order, since **Elliott's (1989; 1994)** work is the only study of this kind that appears in the quantitative ecology literature.

Another factor that may play a role in determining how far upstream fish presence will actually occur is the natural recurrence interval of major debris flows in a basin. The steep, dissected mountains of the Pacific northwest favor episodic debris flows (**Eisbacher and Clague 1984; Swanson et al. 1987**) which typically initiate in hollows at the heads of 1st-order basins (labeled *source area* in Figure 6). These debris flows catastrophically scour headwater channels, often down to bedrock (**Benda 1990**), depopulating them (presumably) of any fishes that might have been present in the process. Materials carried by these flows accumulate further downstream at tributary junctions and breaks in channel gradient, where they fill, block, or divert the channel and often bury fish habitat. Over succeeding years, this material is transported slowly downstream in the form of irregular waves of bed material that diminish in volume and amplitude during their passage.

Although these major debris flows can be catastrophic when they occur, they may not be as bad for the overall long-term health of the system as the description above might suggest. They could, in fact, be thought of as "system resetting" events that revitalize the system (**Benda 1990, 1994; Reeves et al. 1995**). This is because a stream channel that remains undisturbed over too long a period eventually becomes depleted in the supply of bed material and large organic debris it needs for construction and

maintanence of fish habitat, and over time its fish population declines. The new material brought down by catastrophic debris flows replentishes this supply. Over time, new habitats are created in the downstream reaches and new sediment and organic debris gradually replaces that scoured away in the headwater channels. Fish recolonize these new habitats and system productivity increases, until it peaks once more and again begins the slow tail-off that precedes the next major "system-resetting" debris flow.

How often do these "system-resetting" events occur? In this region, they parallel the natural frequency, size, and spatial distribution of stand-replacing wildfires—first the wildfire, then, following within a few years, the major debris flow. Various researchers have published estimates of the recurrence interval of stand-replacing wildfires for different parts of the Pacific northwest. To provide a sense of the time scale involved, **Benda et al. (1999)** gave a value of every 500 years for the coastal rain forest of Washington; **Agee (1991)** estimated 230 years for forests where Douglas-fir is dominant; and **Benda et al. (1999)** listed 100 years for the drier forests of eastern Washington.

So the time scale for these events is anywhere from one to five centuries. As for where they are likely to occur, that appears to be a hit-or-miss pattern across the landscape. Thus is created a range of channel conditions within and among our watersheds **(Benda 1990, 1994; Reeves et al. 1995)**, one consequence of which is that only about 60 percent of the streams in the region may be in the productive part of their cycle for fish at any point in time **(Reeves et al. 1995)**. Since fish abundance depends on just where in the disturbance-reset cycle the stream happens to be, and upstream extent of fish distribution may depend on the ability of fish to survive such disturbances in place or to recolonize as new habitat is created during the recovery phase, the natural disturbance cycle for a basin may be a factor in determining the probability of fish presence at a site.

Three studies **(Lamberti et al. 1991; Scarlett and Cederholm 1996; Serdar 1999)** have addressed fish population recovery in Pacific northwest streams following catastrophic debris flows. In the **Lamberti et al. (1991)** study, the trout population in the disturbed reach recovered to levels equal to or exceeding an undisturbed upstream control reach by two years after the debris flow. In **Scarlett and Cederholm's (1996)** study, the population rebounded quickly as well, but to only about 50 percent of the pre-disturbance level, where it stabilized and held over thirteen years of monitoring. **Serdar (1999)**, on the other hand, reported a population recovery rate similar to **Lamberti et al. (1991)**. Only **Lamberti et al. (1991)** appears to have studied the nature of recruitment ot fry to the disturbed reach, and they concluded from this that density-dependent mechanisms governed the recovery of the fish population at the site. However, although the **Lamberti et al. (1991)** site was inded in an upper tributary of its basin, it was located well downstream of the upper extent of fish distribution in that

stream. So once again, because of the evidence from **Elliott (1984, 1994)** of density-independent mechanisms governing headwater fish populations, one has to wonder if these results describe the recovery of uppermost populations following catastrophic events. More research would be helpful.

A third factor that may play a role in determining the extent of upstream distribution of fish is the climate pattern of the region where the stream is located; i.e., how often drought years occur and the time *interval* between them. The hypothesis here is that in drought years, the upstream extent of usable habitat shifts downstream due to drying up of the water in the headwaters of the *catchment* (**R. Bilby, National Marine Fisheries Service, personal communication 2000**). Usable habitat would shit back upstream as the affected reaches are rewatered following the drought, but fish may only gradually recolonize them. This is only a hypothesis at present with no research to support it, but it is one that may be testable with field work.

Some Methods Employed and Contemplated for Delineating Uppermost-Fish boundaries

As stream typing in Washington still depends, in the end, upon the presence or absence of fish, it is of interest to consider ways that have either already been employed or that one might contemplate using to delineate that point, aside from sending teams of stream typers equipped with electroshockers into the field to discover the uppermost-fish point directly (a method which is, to say the least, labor-intensive).

In Oregon, the probability of fish use based on basin area has been used with reach gradient and reach type interjected as additional criteria (**Lorensen et al. 1993; Andrus 1995; ODF/ODFW 1995**). In this approach, charts of basin area vs. probability of fish presence, like those shown in Figure 7, were generated for each ecoregion of the state. These are used to make the first cut on fishbearing water boundaries. Early-on, however, Oregon recognized that the upper extent of fish use of steep streams can depend on both *reach type and reach* gradient (e.g., step-pool morphology can harbor fish in steeper reach gradients than can bedrock morphology) (**C. Andrus, Oregon Department of Forestry, personal communication, 1995**), so reach gradient and reach type are used to refine calls. This is not strictly a desktop exercise, since field verification is often required to check on reach types and gradients.

Virtually all other methods involve a modeling approach, some employing instream flow data, others using habitat variables, and still others using both. Since at least 1950, biologists and managers have been developing models, usually to predict standing crop or abundance of stream fishes. **Fausch et al. (1988)** reviewed 99 such models developed between 1950 and 1985. Most of these were regression

models incorporating as few as one to as many as 21 input variables—*variables that included details* on basin morphology, channel morphology, flow rates, habitat structure, species biology, and other physical and chemical measures. Common to many of the models were (1) stream size (mostly as measured by drainage area but wetted width and stream order also have been used), (2) gradient, (3) climate (as measured by elevation, water temperature, or precipitation), and (4) the likely availability of nutrients and energy (as measured by various water chemistry tests).

Most of these early models were found *wanting for one reason or another*, such as limits on the range of habitat data included, inclusion of nonindependent variables, or inclusion of subjective and/or derived variables (**Fausch et al. 1988**). Moreover, those with coefficients of determination of 75 percent or better (i.e., the model accounted for 75 percent or more of the variation in fish standing crop) lacked generality. That is, they were good for only a relatively small geographic area—sometimes only a single watershed.

But *the work has continued apace*, using newer insights into fish/habitat relationships, fresher understanding of the form and function of watersheds and streams, and, as they have developed, newer more sophisticated techniques such as GIS and digital elevation models. More recent publications include **Reeves and Everest (1986)**; **Lanka et al. (1987)**; **Scarnecchia and Bergersen (1987)**; **Fausch (1989)**; **Kozel and Hubert (1989)**; **Kozel et al. (1989)**; **Bozek and Hubert (1992)**; **Gagner (1997)**; and **Kruze et al. (1997)**. Many of these newer models still suffer from the same limitations pointed out by **Fausch et al. (1988)**, including lack of generality (**Marcus et al. 1990**), but *they do show good* applicability to the specific range of habitat conditions they address, in the specific areas for which they were developed.

As noted, the majority of models in the publications cited above were intended to predict fish standing crop, not the upper extent of fish distribution—although they could do by asking the model to predict where fish standing crop equals 1. An exception is a regression model developed for coastal and interior watersheds of northern California by R2 Resource Consultants (**Gagner 1997**). This model was developed to predict the breakpoint between California Type I and Type II waters. In California, Type I waters are fishbearing, and Type II waters are not, so in effect this model does predict fishbearing water boundaries. Four variables were included in the model: drainage area, slope, precipitation, and aspect, and the model correctly predicted the Type I–Type II boundary about 70 percent of the time. Although this was deemed accurate enough for the purpose intended, it was felt that greater accuracy could have been achieved by including additional variables (**Gagner 1997**).

In Washington, a modeling approach is also being embarked upon as a desktop means of predicting the upper extent of fish distribution. The model currently in development includes as input variables basin area, reach gradient, elevation, and basin-average precipitation (**B. Fransen, personal communication 2000**). The model was developed by feeding information from field-verified fishbearing water boundaries into a GIS program using 10-m digital elevation data. The model is now undergoing tests in which it is asked to predict fishbearing water boundaries in a number of additional streams that have not been typed. Field verification is then used to determine the accuracy of the model predictions. In its current form, the model makes the correct call in about 95 percent of the tests, and errors are about evenly distributed both pro and con, i.e., the model signals a fishbearing water boundary that is not subsequently found about as often as it fails to call a true boundary that is later found (**B. Fransen, personal communication 2000**).

Summary

- Stream flow, basin area, reach morphology, reach gradient, and microhabitat type are among the principal factors affecting upstream distribution of fish. Natural fluctuations that occur from year to year in fish abundance and the natural disturbance cycle of the stream system may also come into play, although these factors may require density-dependent responses on the part of the fish which may not apply to density-independent headwater populations. The climate pattern of the region where the stream is located, particularly the drought interval, may also be a factor. This is a hypothesis only at present with no research to support it. Field work is needed to understand each of these factors better.

- Aside from the State of Oregon, which relies on the probability of fish presence based on basin area, virtually all other approaches to delineating upper extent of fish distribution involve regression modeling to predict fish standing crop. Common to most of these models are variables that incorporate stream size, gradient, some measure of climate, and some measure of likely availability of nutrients and energy. Although coefficients of determination are better than 75 percent in many cases, the best models appear limited to just the specific areas for which they were developed.

- Washington is developing a model using input variables of basin area, reach gradient, elevation, and basin-average precipitation. Coefficient of determination for the current model is about 95 percent and errors are about evenly distributed both pro and con, i.e., the model signals a fishbearing water boundary that is not subsequently found about as often as it fails to call a true boundary that is later found.

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